THE SOCIAL WORLD OF THE ANTS

by AUGUSTE FOREL

THE SOCIAL WORLD
OF THE ANTS

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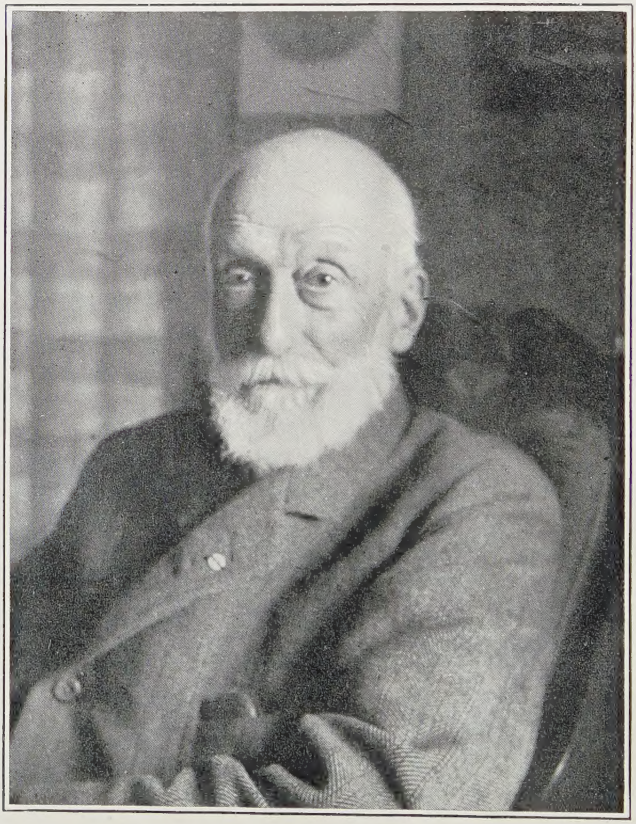

AUGUSTE FOREL.

Frontispiece Vol. II.

THE SOCIAL WORLD OF THE ANTS

COMPARED WITH THAT OF MAN

BY

AUGUSTE FOREL

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PART IV

Part IV

INTRODUCTION

In Volume I we described the bodily structure, sensa-
ions, psychology and dwellings of ants, as well as the
outine within their nests and the various guests and
arasites which infest them. We have now to discuss their
utside relations with others of their own kind, that is, with
ther ant-communities. Here, alas ! we are inevitably
eminded of the horrible massacres which sapped the life-
lood of humanity some ten years ago in the human world-
ar. I trust that we may learn from this tragedy such
ractical wisdom as will disgust us for ever with the
isane wars between man and man, mostly waged in the
ame of national chauvinism, falsely termed patriotism.
his is the sentiment which stirs up passions of hatred in
oor working-men who desire with all their heart that
eace shall reign between the nations ; the chief advantage
f it all is reaped by infamous profiteers and usurers,
dividual or collective, whose sole aim is to gain money at
e expense of their neighbours or of other nations.

Among the ants and termites, however, wars have a
tally different character. They are exclusively collective,
uels and individual battles being practically unknown.
Moreover, war between more than 3,000 distinct species, a
rge number of genera and five sub-families, whose

members differ greatly in size, not to mention races and varieties, is more like war between mice, men, wolves or elephants than war between man and man. We must also excuse the ants on the ground that they cannot embark upon the seas, and that no mariner's compass or Christopher Columbus has ever given them any idea either of the relative pettiness of our earth, or of its humble condition as a satellite of the sun, or of any 'world-wide formicity' which might be conceived as a result of such knowledge. We must not forget that 500 years ago we were almost equally ignorant, and all races of men believed that the universe revolved round themselves. Lastly, ants are guided almost exclusively in their war-making by a collective instinct for the conservation and nutrition of their formicary. Plastic adaptation, acquired by individual memory, plays but a modest part in the matter. At the same time, this part is not negligible; of this we have irrefutable proof in the fact that the alliances made by one species may vary according to circumstances. Hence we must take all these fundamental differences into account when comparing ant-wars with our own ; ants are not men.

While the termite-wars so well described by Professor Bugnion in the appendix to this Volume are purely defensive the wars which ants wage against termites are always offensive, and those they wage among themselves are offensive or defensive, according to circumstances.

Part IV will be divided into seven chapters:—

I The first refers to a few fundamental experiments of my own, carried out before 1874, with regard to natural and artificially induced alliances between ants.

II This is followed by a summary of the remarkable experiments of Miss Adele Fielde on the gradations of friendship and hostility in ants according to odour, age, sex,

species, etc. Miss Fielde has made a very profound study of the details of this question.

III Our third chapter is devoted to the ordinary wars, offensive and defensive, which take place between ants, whether of the same species or different species, but of different communities or formicaries. These wars vary widely in intensity and bitterness according to the adaptations of instinct and according to circumstances, and form transitional stages to alliances and parabiosis.

IV The theme of our fourth chapter is the warfare waged by ants against other living creatures. For most of the facts concerning wars against the termites, however, I must refer my readers to Professor Bugnion's Appendix. He is no more of a Bolshevist than I, but I believe in Socialism—and herein we differ.

V The fifth chapter acquaints my readers with the curious cases of *parabiosis* which I discovered for the first time in Colombia in 1896.

VI *Lestobiosis* or collective synechthry is discussed in the sixth chapter. This also may take place between ants and termites.

VII Finally, in chapter seven, we describe the slave-making instinct in ants, which is very different from human slave-making. For the discovery of this instinct we are indebted to Pierre Huber and his admirable researches of 1810.

We shall then realize more clearly the falsehood of Cæsar's too-famous utterance: 'If you want peace, prepare for war!'—a thousand times no! If you want peace, prepare for it by disarming all men and organizing them in accordance with a true labour socialism of peoples that elect for themselves a supernational authority, supervised by them and responsible to them. We should accomplish this by

means of an international alliance based upon that of the polycalic formicaries and combined with that of the mixed colonies. Even then, we shall still have enough natural enemies outside the human race, and enough work within it to keep the national and supernational police quite busy.

Chapter I

ALLIANCES BETWEEN ANTS

In order to understand the reason for wars between ants, we need to study the reason for their alliances, whether between different formicaries of the same species or between different species and even sub-families. While discussing guests in Chapter IV of Part II, we have seen various ants adopting and feeding all kinds of beetles, flies, crickets and mites, and sometimes rearing their brood. There is nothing strange, therefore, in the fact that they make alliances from time to time with those of their own kind, and set up mixed formicaries.

As a young man I made a number of observations and experiments on this subject, which was then in its infancy, and wrote down my results day by day. In 1874 I incorporated them in my book on *Les fourmis de la Suisse*, the second edition of which appeared in 1920 at Chaux-de-Fonds (Le Flambeau). My readers will pardon me if I here reproduce the most important of these statements.

1 ALLIANCES BETWEEN YOUNG ANTS. Taking as my starting-point the fact that newly-hatched ants are often stolen during the nymph stage by slave-making ants, and that they cannot afterwards distinguish between enemies and comrades, I devised the following experiments :

"I decided to place in a glass-covered box young ants of three different species, giving them naked nymphs and

cocoons of six species to care for. They had to be chosen very young and placed close together, as in certain species three or four days of life suffices to give a newly-hatched ant some power of recognizing an enemy. Hence I put into my glass-covered box well-matured nymphs of *F. pratensis*, *exsecta*, *fusca*, *rufibarbis*, *sanguinea* and *C. æthiops*, and left them in charge of some young ☿ of *exsecta*, *sanguinea* and *rufibarbis* taken from various formicaries. In a corner of the box I put some damp earth, and above it a piece of glass. After a short time the young ants of the three species, working in harmony with each other and showing no inclination to quarrel, carried nearly all the nymphs under the piece of glass and there set up a common establishment. One of the *rufibarbis* ☿, slightly older (darker) than the others, kept apart from them and established herself at the other end of the box with a cocoon. I tried several times in vain to make her come near the others; she persisted in shunning them and returning to her corner with her cocoon; in the end, however (but not until the next day) she decided to join forces with these 'enemies,' as she could not avoid them.

When the experiment had continued for a few days I had the pleasure of seeing new young ants hatched in my box, and on watching attentively I saw some *F. exsecta* and *rufibarbis* occupied in opening a few cocoons, drawing out a nymph from each and aiding her, by means of delicate manipulations with their mandibles, to rid herself of her old skin. Some *F. exsecta* were the first to see the light, but I soon beheld some *F. rufibarbis* opening cocoons of *F. fusca* and *F. pratensis*. In general, however, it was apparent that every kind of ant preferred to bring out nymphs of her own species. Only the cocoons of *C. æthiops* were neglected; the young ☿ did indeed open one or two of them, but the

nymphs inside perished. I thus had the pleasure of seeing a small formicary come to life under my eyes, under conditions of extreme artificiality, consisting of five different species living together on the best possible terms. This experiment gave me occasion to observe that among the nymphs of *F. pratensis* which the ☿ drew out of their cocoons, some were still almost white and others already very dark, of a black or yellowish tint; there were also some of intermediate colours. They all flourished to an equal extent, but the darker ones almost immediately became robust, energetic ants, whereas the others remained weak and idle for several days. This fact, which I have frequently confirmed since then with other species, seems to prove that ant-nymphs are able to hatch at different degrees of maturity; there is no fixed moment of hatching, before or after which success would be impossible, but the workers bring them forth at will, sometimes earlier and sometimes later, to suit their convenience.

About ten days after the experiment began, several of the first ☿ of my box had already become darker. I was then obliged to absent myself. Before setting out I placed my formicary in front of a crack in the wall, wherein the ants hastened to install themselves. I then went in search of some more young workers of *F. fusca* and *pratensis*, in the hope of reinforcing this community of my own rearing. But the newcomers were never welcomed; when they tried to get into the nest, the older inhabitants first threatened them with their mandibles, then seized hold of them, dragged them a certain distance away and abandoned them. Several times did I replace these new ants in front of the nest in vain; the old ones rejected them every time with the same show of anger. Most decidedly, therefore, they had formed an independent formicary."

2 ALLIANCES BETWEEN ANTS OF THE SAME SPECIES BUT OF DIFFERENT FORMICARIES. In 1874 I wrote as follows on this subject:—

"Ants of the same species but of different formicaries will fight to the death when the two parties are separated from one another, placed under favourable conditions, well established and left in freedom, without anything to worry them; the combat becomes half-hearted or spasmodic when one of the two, at any rate, is placed under difficult circumstances, and then it usually ends in a definite alliance; when the circumstances are the worst possible, and especially when there are only a very few workers to each formicary, no combat takes place; the alliance is immediate, or almost so. Once an alliance is made, it cannot be unmade. There are exceptions, however, to all these generalities.

a One summer evening in 1858 or 1859, I filled a bag with some *F. pratensis* taken from seven or eight formicaries a great distance apart, and on returning I poured them all out at the foot of a lilac-tree. By the next day they were all working harmoniously together and founding a common nest. A few days later, I filled a new bag from another formicary of *F. pratensis* and deposited it near the lilac-tree, by the side of the others. A fierce combat began almost immediately; some of the newcomers were killed, while others fled with their cocoons and sought another home.

b On March 8th, 1868, I found two nests of *Leptothorax acervorum;* I managed to remove in one piece the bark containing the first nest, which I will call A, but was unable to obtain possession of the second, which I will call B, except by gathering the ☿, the fertile ♀ and the larvæ in a handkerchief. B, however, was larger than A. On arriving home I covered my table with a cloth, placed in the middle of it the piece of bark containing the A *Leptothorax* and poured out

the others beside it. The A *Leptothorax* were somewhat timid, and clung to the bark; then when the B ants found that they were one family on this cloth, they hastened to invade the piece of bark, in which they soon discovered small openings leading to nest A. They immediately worked their way in and transported their larvæ thither. At first not a single A ant was seen to emerge and show any resistance but the scene quickly changed, and I saw several *Leptothorax* coming out of holes in the bark, and struggling to draw others along by the legs. One of the armies, and I ascertained definitely by various signs that it was B, held the upper part of the nest, for several of its ☿ were occupied nearly all the time in pulling one member of the other party away from it, and the B continued to take their larvæ into the nest. These combats were not of a lively character; no stings were brought into action, and moreover, as this species is extremely tough and robust, the champions actually sustained no injuries worth mentioning. Soon, however, I saw more and more clearly that the B's were engaged in dragging out of the nest, one by one, all the A ants, including the females, with the obvious purpose of establishing themselves in their place. But the A's, not knowing whither to turn, refused to run away and tried instead to return to their nest. This fact occasioned some very comical scenes. The B's, exasperated to see that the A's were hurrying back to the nest as soon as they were released, took to seizing them one after the other by the thorax or a leg, carrying them a long way off, as far as 3 or 4 centimetres from the piece of bark, and depositing them, probably supposing that they would not dare to return. Feeling themselves to be weaker than their foes, the A's folded up their legs and antennæ and allowed themselves to be carried. But directly they were free, they walked straight back to the nest, often arriving

as soon as those which had borne them. I watched this process with amusement for some time, and I noticed that the B's were carrying the A's to greater and greater distances. At last a B arrived with her burden at the edge of the table. Here there was plainly a sheer precipice before her, and she therefore stopped short. I saw her thrust out her head towards the gap, lift the A worker she was carrying, still with folded limbs, open her mandibles and drop her on the floor. She then waited a moment longer and returned the way she had come. I carefully picked up the A ant, which was already running about on the floor, and placed her back on the table in front of the B worker, which was journeying home to the nest. As soon as the B perceived her, she seized her and bore her once more to the edge of the table, stretched her neck yet farther forward than she had done the first time, and threw or rather dropped her enemy to the ground again. I repeated the experiment twice more and obtained the same result; the undaunted B *Leptothorax* set about her task again every time.

I then placed the piece of bark, with all the ants scattered over it, in a glass flask. The fight continued for several days inside the flask, exactly as described above. The A's which were turned out of the nest by the B's returned to it every time. Two or three A ☿ even sustained fairly severe injuries, their legs and antennæ being cut off. Little by little, however, the B's discarded their unavailing rancour and gazed with a puzzled air at the A's in their nest (which they did not kill inside the nest, for in that case I should have seen them throwing out the corpses as they always do under the circumstances). But their fury was concentrated upon two fertilized A ♀, one light and the other dark in colour, and upon three or four ☿ which they dragged about and harried unceasingly. I saw a B *Leptothorax* carrying

one of these ♀ for several hours round the bottom of the flask without depositing her. Down in their prison, these few hapless victims wandered disconsolately about; the dark ♀ and one or two ☿ soon died. Eight or ten days later the light ♀ was left alone, and even admitted into the nest; henceforth I saw her go in and out without molestation, and all brawling thereupon ceased."

c During a fierce fight between three *Formica pratensis* formicaries, A, B, and C, in which a number of ☿ from each party were killed, and which was terminated by the defeat and flight of the B's and C's, I made the following counter-experiment:—

"While the combat was raging, I took four A ☿ from the part of the column nearest the nest, so that I could make sure what I was doing, and three C ☿ chosen with the same care. I put these seven ants together in a glass flask. No fighting whatever took place, but they first separated into two groups, the three C's on one side and the A's on the other (I recognized them by their size, as I had chosen them for this purpose). I then shook the flask in order to mingle them; they ran over one another, without displaying either anger or fear, and then separated into two new groups, one consisting of three A's and the other of three C's plus one A. These two groups remained separate for two days, one of the A's standing faithfully beside the C's, and on perfectly good terms with them. I then placed them all in a small vase, where they united in one group and lived together amicably till the end, without even a preliminary quarrel.

The *pratensis*, A, B, and C, were all true *pratensis*; I examined them carefully, and found that formicary A differed from the others only in containing more small and medium-sized individuals than the two others.

The formicaries of *F. sanguinea* are not very large. As I

have often required a large number of these ants, it has been my lot on scores of different occasions to fill a bag with five or six different formicaries and empty it in some meadow, generally near the nest of another species. I have then frequently observed the *sanguinea* of the different formicaries pulling each other about and even engaging in fairly sharp individual combats, but this performance nearly always ended in a complete alliance. On the other hand, when I carried the *sanguinea* of one colony and put them near to the nest of another, battles took place between them as between the A, B and C *pratensis;* each time this happened there was a fierce struggle resulting in several casualties, and the newcomers were forced to flee."

3 ALLIANCES BETWEEN ANTS OF DIFFERENT SPECIES. First of all, I should like to quote here the normal circumstances of a petty war which proves that mixed formicaries do not always arise from the parasitism of the fecundated queen, the founder of a colony, upon another species.

"Thirty paces away from a large *sanguinea* formicary with which I had long been acquainted, a very small *pratensis* formicary had recently been established beside a vine. One fine day, I stopped near the *sanguinea* and saw that a thick column of their ☿ was filing in the direction of the *pratensis* nest; I followed them, and soon perceived some *sanguinea* ☿, coming back laden with enormous ♀ or ♂ cocoons, which could not have belonged to *F. fusca* or *F. rufibarbis*. I ran to the nest of the *pratensis*, and was just in time. The dome was covered with *sanguinea*, and the whole *pratensis* colony was being completely routed and driven into the middle of the vine, with its fertile ♀ and a few cocoons which they had saved from the plunderers. The *sanguinea* pursued them hither as I watched, snatched away their last cocoons and completely dispersed them.

They then ate all these cocoons, probably because they were ♀ and ♂. I am of the opinion that if the *pratensis* had possessed ☿ cocoons at the time, the *sanguinea* would have hatched them and the formicary would have been mixed."

We will now pass on to experiments which prove how things really happen.

"As early as 1861, in the summer season, I unwittingly prepared myself a surprise for the following year. On various occasions I carried bags full of *F. pratensis* and their cocoons near to some *F. sanguinea* colony, to observe their battles. I noticed that the *sanguinea* invariably won, carried off all the *F. pratensis* cocoons with quite unusual rapacity, and bore them to their nest. I then supposed that they would eat them, as I had already frequently observed this when cocoons of one species were given to another species. Nevertheless, when I visited these *sanguinea* colonies a year after, I was greatly surprised to see the surface of their dome covered with *F. pratensis*. I could scarcely believe my eyes when I saw these two species, usually such bitter enemies, running side by side above the same nest, helping one another to repair the breach I had just made, and together bearing cocoons to their subterranean passages. But in addition to this, the nests still contained the ordinary auxiliaries of *F. sanguinea*, namely *F. rufibarbis* in the one case and *F. fusca* in the other. This fact was worth looking into, and I resolved to sacrifice one of my mixed tribes in an experiment. I filled a large bag with strange *F. pratensis*, and poured them out in front of one mixed formicary containing less *pratensis* than the other. A violent battle then ensued; the *pratensis* which were allied with the *sanguinea* fought on their side against the newcomers, and showed as much fury as the *sanguinea* themselves. The *pratensis* I had brought were so numerous that they won the

day and laid siege to the allies on their dome. Feeling that their cause was lost, the mixed colony took to flight, carrying away their larvæ, nymphs and young newly-hatched ants. I saw the *pratensis* of this formicary running away in company with the *sanguinea*, and helping them to carry the brood. Together they settled some distance away and built a new nest in common. I afterwards repeated these experiments more than twenty times."

The following example is worth quoting here:—

"A *sanguinea* formicary was situated beside a hedge, ten paces away from a *pratensis* formicary, with which it was constantly fighting. These two colonies, however, remained facing each other for several years, and neither of them decided to make a move. One day in 1866, I took a large bag full of these *pratensis*, chiefly cocoons, and placed it in front of the *F. sanguinea*. The *pratensis* were defeated and their cocoons stolen. By 1867 the *sanguinea* formicary was mixed; a large number of *F. pratensis* were working with the others in complete harmony. Now these *F. pratensis* were only ten paces away from their sisters, the *pratensis* of the neighbouring nest, which were also hatched from the previous year's cocoons. This fact was interesting. I took a handful of *pratensis* from the natural formicary and placed them in front of the mixed formicary. A good many of their sisters, the allies of the *sanguinea*, happened to be on the dome at the moment, and these ants attacked the newcomers furiously, covering them with poison, biting them and killing them in a very short time. The battle was extremely violent; I have never seen the *pratensis* of these mixed nests show such combative fury as on this occasion. The many *sanguinea* which rushed to their assistance displayed more moderation in their fighting. I saw several pairs of *pratensis* battling until both lay dead on the field,

after drenching each other with poison. This fact is too clear to need comment. It adequately explains why the *F. pratensis* of the mixed colony had not returned to the formicary in which they had first seen the light and been tended throughout their larval stage and part of their nymph-stage. On April 15th, 1868, the *sanguinea* formicary was still mixed; I made the same experiment again, with an identical result. The natural *pratensis* were always found in their old nest, the mixed colony in their own."

4 FORMICARIES WHICH NATURALLY REMAIN MIXED. The formicaries which I made in this artificial way, but left in the natural nests, usually ended by becoming entirely *sanguinea* once more, even when I provided them with fresh *F. pratensis* cocoons, for they eventually ceased to rear them and simply devoured the nymphs inside. But sometimes the reverse happened, and the mixed formicary became entirely *pratensis*. This may, perhaps, be explained by the fact that I had often given the *sanguinea* some ♀ and ♂ *pratensis* cocoons, but I do not wish to indulge in suppositions; the positive fact is sufficient. One *sanguinea* formicary which had been mixed with *pratensis* became pure again one year and mixed again the next when I gave it some fresh *F. pratensis* cocoons. Having discovered one day a mixed formicary of this kind, containing an almost equal number of *sanguinea* and *pratensis*, I was greatly surprised a fortnight later to find none but *pratensis* remaining. I could discover no explanation as to why and how the *sanguinea* had disappeared, and wondered whether they had emigrated on their own account.

For three or four years I gave up experimenting on this subject, but in 1871 I found three mixed *sanguinea-pratensis* formicaries in places where similar ones had existed between 1866 and 1870, in the neighbourhood of Vaux and Morges,

where I had not been since 1866. The first was on the very spot from which the *sanguinea* had disappeared within a fortnight. The second was remarkably large, with several domes to its nest and a considerable number of *rufibarbis* slaves. The third was mainly composed of *F. pratensis*, and was just occupied in migrating to another nest when I re-discovered it. The few *sanguinea* took an active share in the work. It is absolutely certain, therefore, that these formicaries were able to remain mixed for several years, and this seems to contradict the other facts quoted in the preceding paragraph. Furthermore these facts, which seemed to me incomprehensible in 1874, are explained by the longevity of ants as proved by Lubbock, and more especially by Miss Fielde at a later date.

Shortly afterwards, as I was taking a walk at Lägern, near Baden in the canton of Argovie, with my friend, Professor Eugène Rambert, I discovered a fairly large mixed *sanguinea-pratensis* colony. As neither I nor anyone else had made any experiments with ants in this region, this formicary must have been formed naturally as a result of some battle between the two species, in which the *sanguinea* had doubtless vanquished the *pratensis* and stolen their brood, as in the case quoted at the beginning of the present chapter, which I described to my friend Rambert.

The architecture of mixed *sanguinea-pratensis* nests, whether produced by artifice or nature, is merely a combination of the styles of both species. As soon as the *pratensis* predominate, or even equal the *sanguinea* in numbers, the formicary and nest begin to look as though they belonged to *pratensis*, since the ☿ of this species heap up enough movable materials, such as grass-stems used as beams, to cover the whole dome, which accordingly becomes more or less convex. They also begin to close and

open the doors of the nest in the manner described in Chapter VI of Part II. These formicaries preserve a fairly distinctive *sanguinea* character only when the *pratensis* are decidedly in the minority.

5 FORCED ALLIANCES. The following experiment and its curious result clearly prove the influence of accidental circumstances, acquired and not inherited by instinct, on the alliances of ants:—

"On May 26th, 1871, I placed in a flask, supplied with earth, wood and honey, ten *sanguinea* ☿ from one formicary and ten *pratensis* ☿ from another. At first there were two or three very vigorous individual combats, but peace was presently established and all the *sanguinea* occupied one corner of the flask, while the *pratensis* took another. On either side, however, one or two ☿ fell in battle. On May 28th, seeing that the two groups would neither unite nor fight, and were content to avoid each other or present threatening mandibles, I removed the wood and some of the earth; the groups were at once roused to action, and sharp fighting took place; the *sanguinea* rolled on the ground and grappled with the *pratensis*, then the combatants released each other, to begin again shortly afterwards. One *sanguinea* which had been dragged about by four *pratensis* was even killed, and another *pratensis* had her abdomen cut off. Soon, however, peace was re-established and the two groups were formed afresh, each on a fragment of earth. But the *pratensis* had apparently endured very rough treatment, as only four of them were found alive next day, whereas eight *sanguinea* still survived. Yet the two groups remained calm; one *sanguinea* only was constantly tormenting the *pratensis*.

A few days before, I had found in the road an isolated *pratensis* ♀, probably a virgin, since she still possessed the

bases of her wings, though three-quarters of them had been torn off. I had left her in a box and forgotten to feed her. That same day (May 29th) I found her again and placed her in the flask. She was famished, and instead of fleeing from the ants in the flask she approached them in turn and tapped their heads with her antennæ, begging for food. I was astounded to see the *pratensis* show their teeth and drive her away, whereas the *sanguinea* left her alone. She accordingly left the *pratensis* and began to importune a few *sanguinea* by seeking for their heads, licking their mouths and rapidly striking the epistoma with her antennæ, until two of them consented in turn to open their mandibles, thrust forward their mouths and disgorge honey-dew to her. I could hardly believe my eyes: here was an ant placed between individuals of her own species and others of a different species; these individuals were from different unmixed formicaries, and the ant in question made an alliance with those of the other species against those of her own! In fact, from that day forth, an offensive and defensive alliance was actually established between this *pratensis* ♀ and the *sanguinea* against the *pratensis* ☿. I could not see the slightest sign of a quarrel between the ♀ and her allies, among which she was perpetually crouching except when she was walking about the flask and rolling on the ground, which she did constantly, with one of the four *pratensis* ☿, which betrayed still more hostility to her than to the *sanguinea*.

That same afternoon, however, I found another *pratensis* ♀, likewise straying in the road, but completely apterous and probably fertilized. I took her and placed her also in the flask. As I expected, the sight of her brought about a general battle, which was very violent owing to the fact that I had added two new *pratensis* from the same formicary as the others. One *sanguinea* was drenched with

poison, and died within a few seconds; the *pratensis* responsible for the deed suffered almost as much, and died a few moments after. Two other *pratensis* were also maltreated, without having a chance to hurt the *sanguinea*, and they too soon died. All this time, the virgin *pratensis* ♀ (the first) sided openly with the *sanguinea*, and advanced threatening mandibles towards the fertile ♀, which had immediately sided with the *pratensis*, as it seemed that the other should have done. When peace was re-established, the *sanguinea* and their ally remained in possession of the bottom of the flask, while the three remaining *pratensis* (one of which was ill, and soon died like the others) climbed up the glass with the fertile ♀, which remained faithful to them, and strove to escape. Next day (May 30th), another *pratensis* succumbed to the attacks of the *sanguinea*, which realized their power and invariably took the offensive. The happy relations between them and the virgin ♀ increased; they were constantly licking each other and huddling together, whereas the fertile ♀ and the remaining *pratensis* worker knew not which way to run, and cowered against each other. On June 2nd, the last *pratensis* ☿ was killed, and the fertile ♀ cruelly mutilated by the *sanguinea*, which cut off three of her legs at their tibio-femoral joints, and one antenna from the middle of the scape. The virgin ♀, still lively and active, was walking about among the *sanguinea* as though quite at home; for one moment I even saw her allowing the fertile ♀ to cling to one of her legs, but she soon freed herself of her encumbrance."

Another experiment carried out at a much earlier date gave me a very different result. This and many others taught me, while I was yet young, that those generalizations to which the human mind has such a fatal leaning should be avoided like poison:

"On April 11th, 1869, I placed together in a flask:—(1) two *pratensis* ☿ from the same formicary (*Z*); (2) one *sanguinea* ☿ from a second formicary; (3) two *fusca* ☿, slaves from two different *sanguinea* formicaries, (4) one *pressilabris* ☿ and (5) one *pratensis* ☿ from an artificially mixed *pratensis-sanguinea* colony (*X*), in which one of the two *fusca* had also originated. I could easily distinguish this *pratensis* from the others by reason of her smallness.

To begin with, the ☿ of different formicaries avoided each other without fighting, and those of the same formicary united. Soon the two ☿ *pratensis Z* realized their strength and settled at the bottom of the flask, while the others climbed along the glass. The *pressilabris* ☿ fled in terror from all the others, and once, as I was closing the flask, I was clumsy enough to crush her. In a short time, however, the two *fusca* drew near the *F. sanguinea*, though with an air of suspicion and occasional threats to bite. The little *pratensis* ☿ *X* straightway made friends with her *fusca* (of the same formicary) and cowered beside her, but the *fusca* left her several times and made for the *sanguinea*. The latter soon betrayed an ever-increasing aversion for the two *pratensis Z;* every time she met them she showed her teeth; this feeling was reciprocal, for I once saw a *pratensis* seize the *sanguinea* by one leg; their two abdomens were at once coiled up against one another, but the two enemies instantaneously relaxed their hold. Next day there were two distinct groups: (1) the three *pratensis*—for the small one had allied herself with the two *Z*'s; (2) the *sanguinea* and the two *fusca*, in complete alliance, crouching down together. Here the specific instinct, if it may be so called, had over-ruled the formicary-instinct in the *pratensis X;* this was the first time I had seen such a thing happen. But it is not easy to find a name for the instinct which drove the two *F. fusca* to ally

themselves with a *sanguinea* from another formicary, especially the one which had an old-time ally in the little *pratensis*."

All these facts kindled in me a more and more urgent desire to plan some machiavellian experiment which would lead to a better understanding of ant-alliances by forcing their instinct and putting them on their mettle, so to speak. I beg the reader to bear the following experiment in mind, think it over and form an unbiassed judgment upon it; it is worth the trouble :—

"On May 29th, 1871, I decided to carry out, on a large scale, a long-projected experiment. Providing myself with a large bag, I first filled one third of it with a large *sanguinea* nest, then another third with a *pratensis* nest. No sooner were the *pratensis* in the bag than I shook it sharply to move its contents and get the two species thoroughly mixed up. I left them thus for about an hour and then put the bag in direct communication with an artificial nest of steel and glass, still containing the earth-galleries of a formicary which had been there the previous year. All that remained for me to do was to pour in some water. No sooner had I provided them with this opening than I saw through the glass that a crowd of ♀ of both species were rushing into the apparatus, apparently in great excitement, and in complete disarray; several of them were fighting to the death; others already had dead enemies fastened to their legs; most of them were free, however, but on meeting an equal number of friends and enemies in every direction, they showed their teeth at all and sundry and continually edged away, obviously a prey to terror. The *sanguinea* were the first to recover a certain degree of calm, upon which they promptly set to work to move the cocoons into the apparatus, where they greatly outnumbered the *pratensis*. They carried the

cocoons of the two species indifferently. A certain number of large *pratensis* looked as though they were following this movement mechanically, for they also speedily brought cocoons and laid them in the chambers of the apparatus. When a *sanguinea* menaced them, however, they invariably edged away. But the fighting soon lost its violence and presently they ceased to do anything but offer threats and drag each other about, while the ants which had previously been attacked perished one after the other.

So the first day came to an end. Next morning the apparatus, which was too small for so many ants, was crammed with cocoons. A great many *pratensis* and a certain number of *sanguinea* were dead; the rest seemed to be working together harmoniously, as they were carrying cocoons to the same places and very seldom threatening each other with their mandibles when they met. However, certain *pratensis* were still being dragged about by one, two or three *sanguinea*, which always played the active rôle, whereas the *pratensis* remained passive. I then put the apparatus and the bag, which still contained plenty of ants, chiefly *pratensis*, in communication with my large apparatus of wood and glass (Huber system). This construction also contained the earth-galleries of a nest which had been there the year before. After this I was obliged to go away for a day, and when I returned on June 2nd, I found a complete alliance established. The *sanguinea* and *pratensis* had moved all the cocoons into the large apparatus, and had settled there by mutual agreement in almost equal numbers. I saw no more ants dragging others about, but I soon saw a *pratensis* ☿ disgorging food to a *sanguinea* ☿. The corpses left after the first day's fighting had been discarded in the bags and the small apparatus, and I removed both these heaps; I was even astonished to find less than I had expected.

The *sanguinea* cocoons could be distinguished from those of the *pratensis* by their darker colour, and I saw ☿ of both species paying as much attention to the cocoons of the other as to their own. To this apparatus I adapted a manger of tin, containing some honey. Amid all this calm after the storm, however, I soon saw a few *sanguinea* begin once more to drag the *pratensis* about, but they gave no sign of malice and cut off no limbs. By June 3rd, absolute peace was reigning again and was not henceforth disturbed for a moment. These adult ants of widely differing species were completely united, and now formed one formicary. On June 7th, I carried the apparatus to a grass-plot, placed it near a small *F. rufibarbis* nest, and opened it. The weather was cold, and my ants made but a feeble attack, the *sanguinea* leading and the *pratensis* responding half-heartedly. Soon the *pratensis* discovered a cricket's hole and a small abandoned ant-nest about a foot away from the *rufibarbis* nest. They immediately began to move the whole formicary thither, and in a short time the *sanguinea* came amicably to their aid. It was extraordinarily interesting to see these ants, which had been enemies a few days before, carrying one another to a common nest. I noticed the following gradation in the numerical relationships between the bearers and those borne: (1) Most commonly of all one saw *pratensis* carrying *sanguinea*, then (2) *pratensis* carrying other *pratensis*, (3) *sanguinea* carrying other *sanguinea*, and least often (4) *sanguinea* carrying *pratensis*. I saw only one or two couples of the last-mentioned kind.

Another curious sight was provided by the heads of ants slain in the first day's battle, still clinging to the legs of ants belonging to a different species. The following episode is rather quaint: some cocoons had been piled up for the time being in a tuft of grass close to the apparatus, and some

pratensis were busily engaged in removing them to the new nest. One little *sanguinea* ☿, which was mounting guard over the cocoons, was extraordinarily excited. She tried to prevent the *pratensis* from carrying out their mission, and flung herself at the head of each in turn, snatching away any cocoon which had just been taken up and dropping it again immediately, only to grapple with another ant. The *pratensis* left her alone with admirable patience, and always ended by carrying off their cocoons, despite this little creature's anger. I saw a few other disputes of a similar character, during which a *pratensis* and a *sanguinea* rolled on the earth together for a moment, but quickly broke away without using poison. On one occasion only did I see a little *sanguinea* cling to the leg of a *pratensis* and perish there. It seemed as though liberty had rekindled some slight animosity between the two allies! But this lasted only while the removal was taking place, and affected no more than a few isolated individuals of each species; that same evening it was all over, and the allies were living together in the new nest. The removal had occupied one day only.

One more incident of a different character deserves to be reported: a fairly large beetle (*Hister quadrimaculatus*) suddenly came among my ants, and without more ado plunged its head into a large *pratensis* ♀ cocoon. In vain the enraged ants fell upon it, bit it, sprinkled it with poison and sought to snatch away its prey. The *Hister* had folded its four back legs under its gaster, whence it drew them out from time to time to push its prey against a tuft of grass, while its two front legs, buried, like its head, in the substance of the nymph, continued to spread apart as they clung to it and presented an insuperable obstacle to the united efforts of more than twelve big ants. The chitinous armour of the *Hister* was too hard, smooth and round to be

gripped by the ants' mandibles, and all their efforts were unavailing. I helped the ants in various ways, putting the *Hister* continually in their midst, but in vain. It emerged victorious every time with a cocoon almost as large as itself.

By June 12th the *pratensis* and *sanguinea* had built themselves a small dome; they had made no attempt to separate. On June 14th I found the *rufibarbis* nest occupied by my mixed colony. I had missed the moment of the attack; possibly the *rufibarbis* had emigrated of their own accord. On June 17th the formicary was thriving and in perfect harmony; the dome was covered almost entirely with *pratensis*, but it reddened with *sanguinea* as soon as any danger appeared. These two species also occupied the nests, that of the departed *rufibarbis* and the first one, in which my own had settled. I then went away on a journey.

On July 31st I found my ants still in the same condition, and tried some new tactics. I went to the formicary whence I had taken the adult ants of my mixed tribe, two months before, found a handful of *pratensis* and put them in front of the new mixed nest. I observed all that happened with great care. A lively skirmish took place almost immediately between the newcomers and the *sanguinea* which stole their cocoons; but there was no display of violence in the fighting, and no poison was used. The *sanguinea* fell upon the *pratensis*, rolled them over on the ground, and released them instantaneously. The *pratensis* seemed to be at a loss. They evidently felt that they were beaten, but they did not take to flight. One singular thing about it all was the behaviour of the *pratensis* in the mixed formicary. They only came up gradually, avoided their former sisters as much as possible, without fighting, and turned their attention almost entirely to shifting the cocoons in the nest. But the newcomers, for their part, displayed much more violence, of which this

is an example: A large *pratensis* from the nest arrived near the crowd of newcomers and tried to take away a ♀ cocoon; a small ☿ on the strangers' side at once sprang at her head and prevented her from doing so, pulling her by a leg, then by an antenna, and then trying to separate her mandibles from the cocoon. The *pratensis* had difficulty in putting up a defence, and tried to take hold of the cocoon at the other end, but she finally yielded to the other's persistence and went away, although her much more powerful build would have enabled her to win an easy victory had she wished. Soon, however, the *pratensis* of the nest grew bolder and mingled with those of the crowd. As it was impossible to distinguish them except by the signs of hostility they displayed, which gradually became rarer and more feeble, I was very perplexed. True, I saw several *pratensis* lead away others forcibly to the nest, and in such cases it was easy to guess the origin of each. But I also saw some which rolled themselves up of their own accord, with folded legs and antennæ, and yielded to the mandibles of other *pratensis*, which bore them likewise into the nest. What did this signify? Perhaps a *pratensis* from the nest had lost herself, or one of the newcomers had decided to recognize her former sister and allow herself to be carried by this relation. The later course of events inclines me towards the second opinion. I actually put five or six successive handfuls of *pratensis* from the wild formicary near the same nest belonging to my mixed formicary, and the same thing happened every time. Their battles with the *sanguinea* were always much fiercer than those with their former sisters, though no poison was ever used; so far as I could discover, only one *sanguinea* ☿ and two or three small *pratensis* ☿ were killed. On the other hand, just a few of the newcomers scattered and fled in the grass and then, in many cases, came back to the crowd, while several were carried or

led to the nest by their sisters, as well as by the *sanguinea*. I could not trace any attempt on the part of the *pratensis* of the nest to ally themselves with the others against the *sanguinea* —a proceeding which would have seemed perfectly natural, since they had only been separated from the first and allied with the second for two months; their friendly relations with the *sanguinea* were never marred for an instant. But the most curious thing of all was the comparatively mild behaviour of the *sanguinea* towards these new *pratensis* they had never known. This mystery was soon to be solved. On the following day, the proportion of *pratensis* in the nest had obviously increased and was distinctly higher than that of *sanguinea*. There was no more room for doubt; a good many of the newcomers, at any rate, had been admitted to the nest; the question was—upon what footing? The fruits of my attentive observation on the subject are as follow:—

All the *pratensis* tapped each other in a friendly way with their antennæ, and most of them did the same to the *sanguinea;* but there were special scenes which showed quite another aspect of the matter. For instance, one large *pratensis* had already lost a leg and both antennæ; two *sanguinea* ☿ were engaged in torturing her, and she did not offer the sightest resistance; her sole aim was to escape, but the loss of her antennæ prevented her from finding her way. While one of the *sanguinea* was trying to cut off her thigh, the other was intent upon her prothorax and endeavouring to cut it open or separate it from her head, but she could not get at it as the *pratensis* was much larger and harder than herself; neither of them used poison; the affair was a cold-blooded execution. The *pratensis* was even innocent enough to lick the *sanguinea* two or three times. Another case concerned a *pratensis* which was pestered in a similar fashion by two *sanguinea;* so far she had lost only one leg, and was

making occasional feeble attempts to threaten the others with her mandibles, but she was also of an incredibly long-suffering turn of mind (see fig. 96). All the time that the *sanguinea* were biting her, she was continually tapping them with her antennæ and even licking them ingratiatingly with her tongue. Suddenly, however, she managed to escape by an abrupt movement, and instead of betaking herself far away from the nest she rushed with all strength towards the

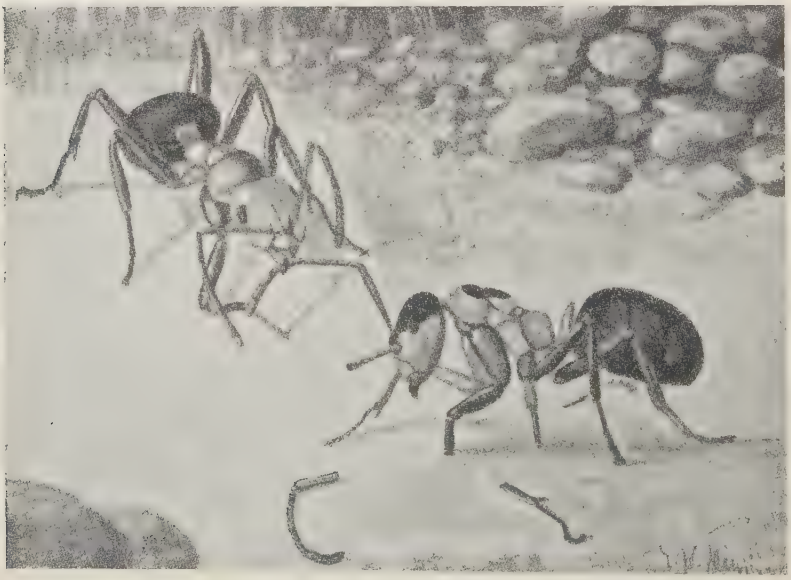


Fig. 96

chief avenue of the nest, jostling as she went against various workers assembled on the dome, and threaded her way along the road, far out of the reach of the *sanguinea*. A moment after I saw a *sanguinea* emerging from the same avenue and dragging a little *pratensis* out of the nest; a second *sanguinea* joined her, but this time the *pratensis* defended herself with sufficient spirit to give a considerable

amount of trouble to the two *sanguinea*, which, however, made no use of poison. I delivered the *pratensis*, which fled with all speed, exactly as the other had done, into the nest. I saw several more *pratensis* dragged out of the nest in this way by *sanguinea*, which afterwards pulled them about on the dome and cut off their limbs. One of these *pratensis*, which a *sanguinea* had seized by one mandible, had the good sense to hang on to one of her enemy's mandibles and roll herself up to be carried. The *sanguinea* tried to unroll her by rubbing her against the ground, but in vain. The *pratensis* would neither move nor relax her hold. Other *sanguinea* tried to bite her, but her stillness seemed to disconcert them. The unwilling bearer grew tired and released her, and she fled in haste to the nest. Last of all, I saw a *sanguinea* bringing out of the nest the corpse of a *pratensis*, still quite young and soft, and deposit it several centimetres away. These expulsions continued for several days, the active part being invariably taken by the *sanguinea* and the passive by the *pratensis*. By August 6th they had ceased, but several *pratensis* corpses and one or two mutilated but still living individuals of this species were scattered around the nest. In accordance with the numerical increase of the *pratensis* element, the dome had assumed the architectural style peculiar to this species and was covered with beams which served to open and close doors. Henceforth I observed no more quarrels, and my mixed formicary still persists at the moment of writing (September 22nd, 1871)."

In discussing (at p. 182 of his work already cited) the theory of the mixture of odours in forced alliances, which I had previously put forward and which was subsequently supported by Miss A. Fielde, R. Brun records his own experiments in which he proved that differences of odour between the two formicaries persist long after the alliances

have ceased. He, therefore, ascribes more importance to the precarious and peremptory circumstances in which the two different formicaries suddenly find themselves than to the diversity of the odours.

The results of the above experiments, especially the last, gave me food for thought. Being afraid of the prejudices of science, which at that time was in re-action against the childish anthropomorphism of the past and therefore regarded all animals, especially all insects, as little more than reflex machines, I felt obliged in my *Les Fourmis de la Suisse* to confine myself exclusively to well-authenticated facts. In many respects, however, these facts still remain a mystery to me. I felt that before the ant-mind could be understood, it would be essential to go deeper into the study of the sensations of ants and of insects in general, and I began to observe them zealously by means of some new experiments. Chapter II of Part II set forth the results of subsequent work in this field by myself and other writers, particularly Brun. But the truth was also reached from other angles. It was realized especially in connection with the foundation of formicaries by fertilized parasitic ♀. Internal anatomy, physiology, secretions, etc., have also enabled us to understand much that was once inexplicable. New horizons have also been opened up, and the experiments of Miss Fielde—to be summarized in the next Chapter—give us a certain amount of knowledge about things which would formerly have been regarded as fairy tales.

Chapter II

EXPERIMENTS OF MISS ADELE FIELDE

We have already made Miss Fielde's acquaintance in connection with the glass observation apparatus (Part III, Chapter I), which bears her name. I should like here to mention a certain number of her splendid and painstaking observations, which have added considerably to our knowledge as to the causes of alliances and wars between ants. The most important of these were carried out in 1903-1904, and they deal with the ants' powers of distinguishing one another. They are as follow:—

In Miss Fielde's opinion, if we wish to show how animals of this kind recognize each other and find their way about, we must turn our attention directly to their guiding senses: sight in the eagle, hearing in the mole, touch in the caterpillar, and smell in the ant. This is very true, as we have seen in Chapter I of Part II, in connection with topochemical smell.

The behaviour of ants proves, moreover, that they associate their perceptions independently of their direct chemical sense. For instance, habit will teach them to outgrow their fear of light, from which they instinctively remove their brood.

When ants are put into an artificial nest, they require several weeks in which to get acquainted with their new dwelling, but they may afterwards be transferred to some

kind of replica of their abode, a Petri cell, a glass house or a wooden box; they will always be comfortable in one of these contrivances, and will quietly resume their accustomed routes over its floors; or they will withdraw into it from a strange environment, even when it lacks their nest-aura.

Miss Fielde divided a colony of *Camponotus pennsylvanicus* into two sections. She continued to fondle the ants of the first section *X* until they felt quite safe in her presence. She trained them to climb on to her fingers and walk about on her hands at their leisure, or even to return to her after wandering for an hour in her room. Not only did these *X* ants cease to bite her when she took them up in her hand, but they became so tame that they would remain quite calmly in their Fielde nest (Part III, Chapter I) for several minutes after the roof-pane had been removed. On the other hand, Miss Fielde deliberately ill-treated the ants of the second section *Y*, lifting them by the leg with a pair of forceps and plunging them for an instant into cold water. Accordingly the *Y* ants soon associated the raising of the glass cover over their nest with a feeling of terror, so much so that they would flee in a headlong panic through the compartments of their house every time she touched the glass.

1 Miss Fielde's Preliminary Experiments (1904)

Miss Fielde wished to show that ants are capable of recognizing certain odours peculiar to their kind after being separated for months, and even years, from those identical odours. To make the evidence plain certain facts which have been well established by previous experiments must be re-stated:—

1 As we have seen, the ants of different natural colonies, whether of the same or of different species and varieties, usually betray a marked aversion to one another when they

meet, and are especially truculent when defending their young. The cause of these perpetual feuds between colonies is the difference in the topochemical odours perceived by the antennæ. Every ant's feelings of fear and hostility are aroused by any ant-odour which she has not yet encountered individually, and which consequently seems to her incompatible with her social comfort.

2 Miss Fielde confirms in every particular that experiment of my own which was quoted at the beginning of Chapter I in connection with young ants gathered and put together only a few hours after they are hatched. They constitute a mixed formicary and live together as friends and allies. Miss Fielde, however, succeeded in bringing about alliances between different genera and even different sub-families (*Formicinæ* and *Myrmicinæ*). She also remarks that all friendships formed in this way are individual, and that every ant acts in accordance with individual experience. The fact that an experienced ant knows the odour of a species or a formicary by no means determines whether she will receive representatives of another species or formicary in a friendly or hostile manner (see Chapter I, section 5: Forced alliances; the first experiment to prove this fact). Among the mixed colonies which Miss Fielde formed in August, 1903, twenty *Aphænogaster fulva* ☿ lived for a year with a fertile *Cremastogaster lineolata* ♀; and the harmony of their lives was as complete as if all the ants had belonged to one species. Representatives of three sub-families: *Formica subsericea* (*Formicinæ*), *Aphænogaster fulva* (*Myrmicinæ*), and *Stigmatomma pallipes* (*Ponerinæ*) lived amicably together in a mixed colony for five months. After the death of the *Stigmatomma*, the *Formica* and *Aphænogaster* continued to live in common on friendly terms for a year. Some *Formica lasioides*, *Lasius latipes*, *Aphænogaster fulva*, *Myrmica*

rubra and *Cremastogaster lineolata* affiliated in one colony for several weeks. Until Miss Fielde disintegrated them, all these mixed colonies and others besides continued to extend their friendship to every ant which bore a familiar odour, and therefore deserved approval, directly she was introduced into the nest. On the other hand, all ants with unfamiliar odours were regarded as strangers and enemies, and accordingly attacked. Even an enlarged acquaintance with ant-odours does not render these insects more tolerant towards unknown odours. Except in established mixed colonies, every strange ant that is introduced, even when she belongs to the particular variety represented by the colony, is excluded from the community and debarred from living there.

In a mixed colony consisting of one species of *Camponotus*, two of *Formica* and one of *Aphænogaster*, all the newly-hatched *Cremastogaster* introduced by Miss Fielde, or even born in that same nest, were killed.

3 Ants inherit odour from the queen from whose eggs they are derived. The fertilized females endow their eggs with a special odour, by which they recognize every newly-hatched ☿ or ♀. This has been proved by Miss Fielde from the fact that an ant which is isolated during the nymph-stage and left until it has been hatched for several days can never have smelled any odour but that of its own body. Nevertheless, directly it is placed near its mother it immediately snuggles up against her, whereas it may attack its older ♀ or ☿ sisters. Miss Fielde presented five fertile ♀ of her species to a young ☿. There can be no doubt that the queen recognizes her own odour in callows that she has never met before.

On July 28th, 1903, Miss Fielde established a colony (N) of *Camponotus pennsylvanicus* in a large Fielde nest. It

consisted of a fertile queen, 2 centimetres long, several scores of workers and a number of cocoons. During the first week in August she laid some hundred eggs, after which she ceased laying until March, 1904. The first larva from one of these August eggs emerged on the 27th of the month, and the first cocoon derived from the same batch of eggs appeared on March 13th, 1904. By April 8th there were some big larvæ in the nest, and also a number of cocoons 5-12 millimetres long. The first cocoon was hatched on April 24th, in a temperature of 24°C. or 76°F. The cocoons continued to hatch until July 14th, when the last one became a young ant. When they were hatched, Miss Fielde separated many of them into special groups. Her experiments with the N colony were as follow:—

EXPERIMENT A. Three large ☿ from the August eggs were hatched each in isolation in 1904 on July 8th, 11th, and 14th respectively. On August 5th, these three ☿, whose ages varied from 22 to 28 days, and which had never met either a fertile ♀ or a ☿ older than themselves, each instantly affiliated with the two other ☿ as soon as they met them. The queen obviously recognized the inborn odour of her young children and snuggled close to them. Each of the three ☿ recognized in the ♀ and in the two others the only ant-odour she had ever known, namely, that of her own body. All these happenings were observed through an orange glass, for this colour is practically the equivalent of darkness so far as ants are concerned, as I have proved in my *Sensations of Insects*, and as Lubbock has also proved.

EXPERIMENT B. Four ☿ from the N colony were hatched from the eggs of August, 1903, their cocoons having been segregated between May and June, 1904. By July 6th, these ants, which were 21-25 days old, had never met any other ants of their species. The mother was then introduced into

their nest. All five ants immediately affiliated, and some larvæ put in by Miss Fielde were laid beside the queen-mother. She was at least a year older than the four ☿, and they could not have recognized her except by means of their own odour at hatching time.

EXPERIMENT C. Five *Camponotus* ☿ from the N colony, hatched between April 25th and May 10th, 1904, from the cocoons of the eggs laid in August, 1903, were between 27 and 72 days old on July 6th, 1904, when Miss Fielde placed the queen-mother near them. Within five minutes she had touched antennæ with every ☿ and had become the centre of a friendly group.

EXPERIMENT D. Fourteen ☿ from the N colony, hatched from their cocoons either after April 24th or before May 10th, 1904, and derived from the eggs of August, 1903, had never been in the company of other ants of their species. On July 6th, 1904, Miss Fielde introduced the queen of N, the oldest ☿ of the segregated group being then 73 days old. Great excitement prevailed for a moment in the nest, with some tentative nabbing of the queen; but in less than one minute the ☿ had discovered that she belonged to them. Within a few minutes four ☿ began to lick her, one mounted on her back, and seven others grouped themselves round her.

The behaviour of these ☿ towards their mother proved that her odour had remained unchanged or practically so. Their behaviour towards their sisters was very different, since great diversity in age was represented.

4 Miss Fielde's experiments of 1902 proved that the odour of ☿ ants changes as they advance in age. Of this we will give some examples later on. About forty days usually pass before there is any change great enough to evoke any display of suspicion or antagonism. But in certain cases between forty and sixty days may differentiate familiar

odours to a sufficient extent to prevent ants from associating with one another.

Whenever young ants have been prevented from associating with older members of the same formicary, it is always the younger ones which betray most suspicion or hostility towards the older. Miss Fielde draws our attention to the fact that all the ants employed in her experiments were under her constant care and supervision without the interference of any other person: they spent the summer, from the first of June to the end of September, in the Marine Biological Laboratory in Massachusetts, and the rest of the year in New York City.

Moreover, in all cases of recognition of a new visitor, when nothing is said to the contrary, a small section of the brood had been introduced a few days previously in order to induce some of the ☿ to tend and care for them; for the reaction to a visitor becomes more prompt and decisive as soon as larvæ and nymphs appear in the nest.

Miss Fielde adds that in her work of 1904, of which we have given an account, she did not mention a third source of individual odour, although she always allowed for this in her experiments. I refer to the odour transmitted to other ants with which any individual associates; and which appears and disappears with certain external conditions. In a mixed nest, ants take the odour of their associates, but this accidental odour is dispelled by isolation within about ten days, and is replaced again by the inherent individual odour. Ants which have been smeared with the juices of ants belonging to another species or colony are liable to be attacked by their comrades, which mistake them for enemies.

Miss Fielde submerged ants of two different species or two colonies for eighty hours or more in distilled water at a

temperature of 10°C., using 35 cubic centimetres for a dozen ants. After this ordeal they revived, but when put once more in their former nest they were attacked as enemies by their old comrades. Ten days were not sufficient for the inherent individual odour to re-assert itself, or, in other words, to dispel the mixed odour incurred during submersion. A counter-experiment gave us adequate proof of this matter: when ants of the same colony were submerged in a similar manner, but separately, they were immediately received in a friendly fashion when returned to their former comrades.

Miss Fielde then submerged three *Camponotus pictus* and fifteen *Aphænogaster fulva* for eighty hours. One of the *Camponotus* came back to life and was returned next day to three of its old comrades which were attending to some cocoons in a small Fielde nest. It was immediately attacked and would have been killed but for the intervention of Miss Fielde, who then isolated it in a cell for ten days and then again returned it to its first nest. Two of its old comrades attacked and killed it. A few of the *Aphænogaster*, which also came back to life and were placed in their old nest, were likewise killed by their quondam associates.

Out of four *A. fulva*, which returned to life after eight days' submergence in the company of five *C. pennsylvanicus*, three were killed by their old comrades when put back in the nest. The survivor was isolated in a Petri cell for twenty days before being returned to her nest. She accordingly became the centre of a circle of ants which submitted her to a critical examination for several minutes. A day later she was dragged by two ☿, but in the end she was restored to good standing in the nest.

It is very interesting, as Miss Fielde tells us, to observe the puzzled or critical demeanour of an ant which is striving

to satisfy herself as to whether a newcomer has an incurred or an inherent foreign odour. I can certainly confirm this statement, having said the same thing on countless occasions, as the reader will judge for himself from my experiments quoted in the last Chapter, particularly the last one of sec. 5, 'Forced alliances,' but I was not particularly methodical.

EXPERIMENT E. On July 18th, 1904, Miss Fielde placed a young ant, seven days old, in a separate nest occupied by two ☿ of the N colony, which were taken as cocoons when the colony was still wild on July 28th, 1903, and hatched shortly afterwards—being therefore about eleven months old. After a careful examination, the two older ants behaved in a friendly manner to the younger one, which they evidently recognized by their own early odour.

EXPERIMENT F. Miss Fielde used my old method of marking ants of the same species with a coloured streak, laid on with a brush, in order to distinguish individuals. On July 6th, 1904, the N queen and her fourteen ☿, mentioned in experiment D, were all serenely grouped in their nest. Miss Fielde then introduced into their midst two N ☿ which had hitherto been segregated, and which, having been hatched between August 14th and September 3rd, 1903, were about ten months old, whereas the ☿ living in the nest were only seventy-three days old. The two visitors had previously affiliated only with the N queen and had been approved by her. They were probably the issue of the eggs which she laid in 1903, but they were seven to eight months older than the ☿ inhabitants of the nest, and much larger. Nevertheless, several of the younger ones tenaciously attacked them and dragged them about. The visitors did not retaliate. One of them even tried to placate her young sisters by offering them regurgitated food. In half an hour's time the attacks seemed to diminish in intensity and Miss

Fielde removed the visitors. It is therefore apparent that hostility between ants, like the closeness of their affiliation, admits of all possible degrees.

None of the older ☿ of this last experiment had ever during their lives met others younger than themselves, and conversely, none of the younger ☿ had ever met sisters older than themselves. It is clearly proved, therefore, that we are here concerned with an hereditary instinct for odours, and a variation of these odours according to age.

2 Recognition of Specific Odour (1904)
Series A

Miss Fielde has proved that ants of various species whose history she has recorded have the faculty of recognizing odours which they have not encountered for several months. In August, 1903, she formed a mixed colony with ☿ of *Camponotus pennsylvanicus*, *Formica subsericea* and *Aphænogaster fulva*, all of which were hatched in her artificial nests between August 14th and September 3rd. This mixed formicary is represented in fig. 76, p. 449, Vol. I. Within a few hours of its hatching every ant made the acquaintance of its elders, and this mixed colony was therefore constituted without any dissensions (as in my first experiment in Chapter I). On September 24th, Miss Fielde separated, according to genera, the ants of a single colony, which she had marked A, the youngest of which were less than twenty days old and the oldest of which were more than forty-one days old. She collected all the *Camponotus*, all the *Formica* and all the *Aphænogaster*, and placed the members of each genus in a separate new Fielde nest, which was free from any nest-aura, as it had been rinsed with warm water according to Miss Fielde's method. The nests were marked A1, A2, and A3. She did not allow any of the nymphs to hatch, but whenever

a severe recognition-test was in progress, a few inert young from the workers' eggs or larvæ from another nest were always introduced, temporarily, at any rate. No ant of any species was admitted to either of the segregated groups except as recorded in the experiments.

NEST A1. C. PENNSYLVANICUS. On April 8th, 1904, three large vigorous *C. pennsylvanicus* ☿, with no brood, were in nest A1. Miss Fielde introduced some *Aphænogaster* which had been their companions in September, 1903. The *Aphænogaster* were terrified, and violently attacked by the *Camponotus*. Miss Fielde was obliged to remove them in order to save their lives. It was evident that their odour had changed during the six and a half months that had elapsed, and was unfamiliar in April to their old associates of September, 1903. Some young *Aphænogaster* taken from the same wild nest in the summer of 1904, and some other young ☿ with the same odour as they had possessed at the time of association were killed by the *Camponotus* A1. The *Formica* were likewise refused admittance.

NEST A2. F. SUBSERICEA. These ants had similarly lived on good terms with the *Camponotus* for at least twenty and at most forty-one days, and had been separated from them on September 24th, 1903. On April 8th, the six and a half months of separation were accordingly identical. There were thirty-six *Formica* ☿ and no brood, and Miss Fielde introduced into their midst one of the *Camponotus* ☿ which had originally been their companions. She was immediately attacked, and had to be removed to save her life. This result was therefore similar to that of A1. The *Formica* manifested the same antagonism towards the other two residents of this nest A1.

These *Formica* ☿ continued to reside in their nest, and laid a few parthenogenetic eggs, which were under their care,

when on April 25th, 1904, Miss Fielde introduced into their nest three *Camponotus* recently hatched from the eggs laid in August, 1903, by the mother of the *Camponotus* of nest A1. These young *Camponotus* received an amiable welcome from the *Formica* and until May 10th Miss Fielde added others, which were also young. The *Formica*, now eight months old, continued to live on good terms with the young *Camponotus*, whose odour had been familiar to them during the early days of their life. They regurgitated food to them, allowed them to carry the egg-packet and take care of their larvæ, and treated them in all respects as members of their own colony. No deaths took place during the twenty days following the introduction of the young *Camponotus*, but on June 25th Miss Fielde took them away. These *Formica*, therefore, recognized the ant-odour of another species, once familiar to them, after seven months of separation.

As Miss Fielde had at her disposal no *Aphænogaster* of the same lineage and age as the *Formica* hatched in the autumn of 1923, and therefore familiar to them by odour, she was unable to introduce any *A. fulva* likely to be welcome to them. The *A. fulva* individuals formerly associated with the *Formica* in the A nest had then changed their odour, and the *Formica* refused to affiliate with them.

NEST A3. A. FULVA. The former friendship of *A. fulva* with the *Camponotus* and *Formica* of nest A had lasted as long as that between the other two species, until their separation in 1903. On April 8th, 1904, Miss Fielde introduced into their nest A3, which contained forty-one ☿, a former companion in the shape of a *F. subsericea* ☿ from nest A2; she was fiercely attacked, like other *Formica* of the same nest. A *Camponotus* from nest A1 was received with equal hostility. It was at once evident that the *A. fulva* discovered

a strange odour in every visitor. When the experiment was complete and definite, Miss Fielde removed all these visitors and left the *Aphænogaster* A3 at peace in their nest until April 24th. She then introduced into nest A3 a *Camponotus* ☿ one day old, the issue of an egg laid in August, 1903, by the mother of the ☿ in nest A1, and therefore of those which were attacked and rejected. A few minutes later, three of *A. fulva* began to lick this new ☿, and all of them had viewed her with approval. She received the same devoted care as if she had been a young *A. fulva* of the same colony. That same day, Miss Fielde added two more newly-hatched *Camponotus* of the same line of descent, and they also were lovingly tended until April 27th, when they were transferred to another *A. fulva* nest M.

The *Aphænogaster* M were of the same age as those of nest A3; they were derived from the same colony and the numbers in their nest were almost equal. The only respect in which they differed from A3 was that they had never lived with any *Camponotus*. As soon as Miss Fielde introduced one of the young *Camponotus* into nest M, the large *A. fulva* of this colony attacked them; and although the newcomers were twice as large as they and had a tougher integument the residents harried them to death. The behaviour of the *A. fulva* M, like the contrary behaviour of the *A. fulva* A, was based on the recognition of odour. *A. fulva's* power of recognizing an odour, therefore, extends through an interval of at least seven months.

Series B

A second series B was established on July 20th, 1903, and until August 28th, that is, for forty days, Miss Fielde added newly-hatched ☿ to the mixed colony. This colony consisted of *Aphænogaster fulva* from the C colony (see

below), *Lasius latipes* from another colony F and *Cremastogaster lineolata* from a third colony H. On September 24th, 1903, Miss Fielde separated these ants according to genera; as in Series A, putting each group into a new Fielde nest of its own, where they remained until the end of the experiments, except in the case of ants introduced for experimental purposes. The series was numbered B1 (*A. fulva*), B2 (*L. latipes*) and B3 (*C. lineolata*).

NEST B1. A. FULVA. On April 1st, 1904, six months after their segregation, there were about sixty *A. fulva* in nest B1. Miss Fielde then introduced two *L. latipes* ☿ from B 2, the former companions of the *A. fulva*. The *Lasius* evinced no fear, and the *Aphænogaster* no aversion, but residents and visitors instantly affiliated. The *Lasius* remained safely in the B1 nest for four days. On April 5th, Miss Fielde took the same two *L. latipes* and placed them in another *A. fulva* colony, consisting of two fertile ♀ and sixteen ☿, all hatched in August, 1902, and therefore a year older than B1. They had belonged to the same colony C, but had never been associated with *Lasius*. These *L. latipes* tried to escape or hide, like all ants in a nest of recognized enemies. In this way they succeeded at first in avoiding the *A. fulva*, but when Miss Fielde returned that same evening, they had been killed and thrown out on the rubbish heap.

L. latipes has a strong odour to which human nostrils are susceptible, and it seems as though the *A. fulva* recognized them by this means after an interval of six months. But on June 11th, 1904, Miss Fielde introduced among the *A. fulva* B1 (former comrades of the *L. latipes* B2) two *L. latipes* ☿ of unknown age from the wild nest of the F colony (which had not, therefore, associated with the mixed colony); these were speedily killed, and two more were also killed on the ensuing day.

On August 11th, 1904, a *L. latipes*, recently hatched from another colony K and introduced among the B1, was also immediately killed.

On June 11th, 1904, Miss Fielde went to the old wild *Lasius* F nest in search of a remainder of its population, and secured a few ☿ and four larvæ. On August 4th, the larvæ spun cocoons and on August 18th, the first young ☿ was hatched. She was immediately placed in nest B1, where the *A. fulva* patted her in a friendly fashion with their antennæ, licked her and cared for her among the brood with which they were busily occupied. They had recognized in her an odour from which they had been separated for eleven months.

The *A. fulva* of nest B1 met no *Cremastogaster* between September 24th, 1903, and July 7th, 1904. At that time they numbered fifty old inhabitants and the larvæ from their own eggs, and Miss Fielde introduced into their midst several newly-hatched *C. lineolata* from a wild nest V. In the space of a single day, all these *C. lineolata* were killed and their bodies piled together in a corner of the food-room; on July 9th, others suffered the same fate.

On June 24th, Miss Fielde had taken from the wild nest of the old *C. lineolata* colony H a few larvæ and some ☿ to rear them. Then on July 22nd she had put a dozen young ants, hatched from these larvæ, in the nest B1, whose residents were much engrossed with their own pupæ. Two or three of these visitors were killed and torn to pieces, but the others were accepted into close companionship by the *A. fulva;* they were allowed to walk over or rest on the pupa-pile, and were gently licked, without receiving any hurt during the twelve days for which Miss Fielde left them in nest B1. But on July 25th, one of those twelve days, a strange and newly-hatched *Formica lasioides* introduced into

nest B1 was immediately killed by the *A. fulva* and carried to the rubbish-pile.

The mother of a *Cr. lineolata* nest K was the daughter of the fertile ♀ of the H colony (of the same species), which had given rise to several generations, including the ☿ of nest B3. Miss Fielde placed a few B3 ☿ in nest K with a fertile ♀ of colony H. Never before had this ♀ encountered any *C. lineolata* workers, having spent her whole life since hatching in August, 1903, with *A. fulva* workers. However, both the ♀ *Cremastogaster* and the ☿ *Aphænogaster* took an interest in the *Cr. lineolata* hatched on July 5th, and continued to live on intimate terms with them. The K mother had therefore retained the odour of her own H mother, and the young ☿ bore the odour of their mother, unchanged by ageing. The *Cr. lineolata* in question was therefore derived from the mother whose eggs had produced the B3; this fact alone would prove as much.

When the *A. fulva* had no brood of their own in the Fielde nests, they often allowed the *Cr. lineolata* nymphs to hatch in their midst and live there, though they did not combine with this species to form a mixed colony, and when engaged in the care of their own young, always killed them as soon as they hatched. It appears that the B1 *A. fulva* recognized an old odour in the young *Cr. lineolata* of Colony H, for after ten months' separation they resumed their former friendship with them.

After this, on August 4th, Miss Fielde removed all the *Cr. lineolata* from nest B1, and the *A. fulva* were without *Cremastogaster* for twelve days. On August 16th, 1904, she put back into B1 one of their old *Cr. lineolata* companions of nest B, which had been separated from the *A. fulva* on September 24th, 1903. She was killed within a few hours.

Her odour had not been recognized after a separation of less than eleven months.

NEST B2. L. LATIPES. In April, 1904, so few *L. latipes* remained in B2 that Miss Fielde was obliged to use them all for her experiments with the *A. fulva* B1 and the *Cr. lineolata* B3, until they were exterminated.

NEST B3. CR. LINEOLATA. On April 5th, 1904, more than six months after the segregation of the *Cremastogaster*, there were about fifty workers in their nest, B3. Miss Fielde then introduced two *L. latipes* with which they had lived on friendly terms for about forty days, six months before. The *Lasius* were attacked and would have been killed, had Miss Fielde not rescued them. Despite the strong odour which these *Lasius* possess for us, their old companions did not recognize them. It was at that time impossible for Miss Fielde to introduce any *Lasius latipes* younger than those with whom they had formerly associated. But on August 12th, 1904, she put in a newly-hatched ☿ from another colony X, which was immediately killed by the *Cr. lineolata*. On August 20th, 1904, she introduced into B3 a young *L. latipes* from the wild nest of the F colony, a sister of the one which was placed in B1 on August 18th, and this ant was amiably received. These *Cremastogaster* therefore recognized in the *A. fulva* an odour from which they had been separated for eleven months. That same day, August 20th, an adult *Lasius* of unknown age, but from the same F colony, one of the nurses of the newly-hatched worker lately accepted, was introduced after her, but was killed the following night.

On April 8th, 1904, Miss Fielde introduced two *A. fulva* among the B3 *Cremastogaster* ☿, with which they had lived on friendly terms the previous autumn, and from which they had been separated for more than six months. One of the

visitors showed signs of fear and tried to escape like a stranger; the other fought with a *Cremastogaster*. Change of odour had therefore made enemies of these old friends.

Not until July, 1904, was Miss Fielde able to introduce a few newly-hatched *A. fulva* from the natural nest of colony C and related to the B1 ants. In this natural nest were several fertile ♀. To prevent these young ☿ from bearing the odour of the old ants, Miss Fielde separated several nymphs and offered the *Cremastogaster* none but young ☿ recently hatched from them. But these young *fulva* ☿ were all killed, and their bodies were torn in pieces a few days after their introduction. They were doubtless the progeny of other queens than those which produced the early acquaintances of the *Cremastogaster* in nest B3.

3 Miss Fielde's Hypothesis (1904)

On comparing the data here presented with those of the preceding years, we can represent in diagrammatic form the probability that an ant, isolated since the nymph-stage, will encounter a familiar odour the first time she meets another ant of her colony. If the odour of a queen remains unchanged and is communicated to all the eggs laid by the mother and all her inert young, and from the beginning of the active life of the ☿ there is a progressive change in the inherited odour borne by her, then there will be more than one odour among the ☿ every summer, as all the eggs laid by a queen are not hatched during the summer in which they are deposited. Let us suppose that a young fertilized queen, the founder of a colony, has laid her eggs in her isolated cell in July, and reared her little brood in sixty days. The eggs which she will next proceed to lay in the autumn will not be able to produce larvæ until the end of autumn, and these, in such a climate as ours, will not appear in their adult

ant-form until about June in the following year. By this time, the odour of the first batch of ♀ will already be several months old, and will perhaps have changed so much that it seems unfamiliar to the young, newly-hatched ☿, which know no odour but their own, or in other words, their mother's. And the same will obtain in the following years.

In a Lubbock nest, a fertile ♀ can live for fourteen or even fifteen years, but for the purpose of the diagram, which represents the progressive change of odour in worker-ants, it was assumed that she lives only ten years.

The arabic numerals in horizontal line indicate the number of years lived by a queen, the founder of a colony.

The roman numerals on the left denote successive broods produced by the ♀, here supposed to be the only fertile female of the colony.

The letters symbolize the odour of the ☿ ants of this colony.

DIAGRAM OF THE PROGRESSIVE CHANGE IN ODOUR AMONG ☿ ANTS:

	1	2	3	4	5	6	7	8	9	10
I.	a.b+	a.c+	b.d+	c.e+	d.f+	e.g+	f.h+	g.i+	h.j+	i.
II.	.....	a.b+	a.c+	b.d+	c.e+	d.f+	e.g+	f.h+	g.i+	h.j+ i.
III.	.....	a.b+	a.c+	b.d+	c.e+	d.f+	e.g+	f.h+	g.i+	h.j+ i.
IV.	.....	a.b+	a.c+	b.d+	c.e+	d.f+	e.g+	f.h+	g.i+	h.j+ i.
V.	.....	a.b+	a.c+	b.d+	c.e+	d.f+	e.g+	f.h+	g.i+	h.j+ i.
VI.	.....	a.b+	a.c+	b.d+	c.e+	d.f+	e.g+	f.h+	g.i+	h.j+ i.
VII.	.....	a.b+	a.c+	b.d+	c.e+	d.f+	e.g+	f.h+	g.i+	h.j+ i..

If all the ☿ from the queen's seventh year eggs and possessing the *a* odour had been separated from the others directly they were hatched, the only ones with which they would affiliate immediately would be those derived from eggs hatched during the sixth year. These ☿, if hatched less than forty days apart, would at once affiliate, despite their separation. The ants bearing the odours *b*, *c*, *d*, *e*, *f*, and *g*

would affiliate with all those which still bore the inherited maternal odour *a*.

But when separated from one another, they gradually lose the memory of this odour, and finally cease to recognize it in other ☿ ants.

Obviously the above diagram has no pretensions to be more than a theoretical approximation; but it renders intelligible certain phenomena observed by Miss Fielde in the C colony, which she followed up for four years, not only in natural nests but also in artificial ones.

When a fertile ♀ does not fly away to found a new colony, but remains in the one which gave her birth and adds her progeny to its population, all the members of this colony thereupon receive a more liberal education in topochemical smell. Every ant behaves according to her individual experience of odours, and if this has been restricted, quarrels are likely to ensue. The knowledge of many odours of ants of diverse lineage makes her more tolerant towards her kind. If some of the ☿ be separated from their colony as soon as they are hatched, they may show friendly recognition of younger ants from their old nest, but this will be brought about by an act of memory spanning the interval of their separation. These are the precise conditions produced by Miss Fielde in her colony C.

The C colony was a large, polycalic community of *A. fulva* which lived under stones scattered at considerable intervals over an area 90 yards in diameter, along a lane and pasture.

Miss Fielde was unable to find any other *A. fulva* colony in the neighbourhood. It seemed that a number of young ♀ mated with their own kin and remained in the same colony. She found no less than fifteen fertilized ♀ (de-alated or without their wings) in a single spadeful of earth. As soon

as ♀ and ☿ from the extreme limits of the area in question met, they affiliated at once, without the slightest hesitation.

On August 22nd, 1901, Miss Fielde found under a stone in the middle of this C colony, a number of ♀, ♂ and ☿, which she divided into two sections, placing each in a separate Fielde nest for two years. No young were allowed to hatch during these two years in either section. In August, 1903, however, they recognized each other and at once affiliated; but their affiliation with ♀ and ☿ newly imported from the wild nest was less perfect. Miss Fielde then placed the two united sections, again without young, in a separate nest, where they spent a third year ending in August, 1904, and introduced into their nest some marked ☿ and fertile ♀ taken from their old wild nest. One of the two ♀ was at once received with every sign of friendship, whereas the other was simultaneously licked and dragged by different ☿, but was accepted at the pupa-heap after a few hours. The ☿ were well received. Out of the 114 young ♀ which were then introduced one by one, each after a short interval of rest, only two were attacked. Though all the young ants accepted during this summer of 1904 must have had the odour of the resident queen, it seems highly probable that many of them bore odours which were recognized by the ☿ residing in the Fielde nest after a separation of three years.

During these three years the ants had certainly not met any companions one or two years old from outside their artificial nest. In August, 1902, Miss Fielde separated a queen and some workers, all of which had been hatched that month, and in August, 1903, she did the same with a group hatched later on in the same month. No nymphs belonging to any of these separate groups were allowed to hatch. In August, 1903, Miss Fielde, therefore, had command of four groups separated from the wild nest C: (1) the C nest from

the natural colony C which began its career on June 24th, 1904; (2) the C1 group, exactly one year old; (3) the C2 group, exactly two years old; (4) the C3 group, at most three years old. All four had been acquainted with their seniors before their separation. In August, 1904, the C3's welcomed into their nest ten C2's and ten C1's, and so indicated a perfect recognition, after a long separation, of odours which had not been represented in their nest since the date mentioned.

On the other hand, as soon as Miss Fielde introduced C3 ♀ or ☿ into a nest peopled with hundreds of workers taken in June, 1904, from the wild nest C, or hatched during the summer of 1904, the C3's were always violently attacked. *These ants were now strangers to the younger generation of their former wild nest.* Miss Fielde adds: "The C colony had been much harried in its natural domain, by the rebuilding of stone fences, by repairing of the lane road, and by my own depredations. Ants so old as my three-year-olds have apparently become almost unknown in the wild colony."

The greater the age of the colony, the less chance there is that one of its members which has been separated as a nymph and kept in isolation will recognize her own odour in another ant taken at random from the colony whence she was hatched. In August, 1904, Miss Fielde isolated in this way certain nymphs and the ants which developed from them. The following experiment is typical.

a A ☿ nymph from the C colony wild nest was isolated. When she had been hatched for eleven days, she knew no ant-odour but her own. Miss Fielde then introduced one by one into her Petri cell, where she was absorbed in the care of larvæ given her for that purpose, all the twelve C3's, all the seventeen C2's, all the forty-two C1's and seven C's of exactly her own age, so that the number of visitors which

thus arrived separately from time to time rose to nearly eighty. A rest-period was allowed to intervene between each visit. This young ant violently attacked every one of these visitors, drove them away from the larvæ, and, in some cases, even took them outside the Petri cell, if Miss Fielde lifted the cover. From time to time a visitor would retaliate by attacking the isolated young ant, and Miss Fielde was obliged to intervene to avoid a casualty.

In other experiments of this kind with ☿ hatched in isolation, it often happened that the young creature recognized her own inherited odour in a visitor, which she then willingly permitted to share with her the care of the larvæ. Although the isolated nymphs had been taken from different parts of the C colony, they all behaved in the same way, and one is tempted to think that all those tested by Miss Fielde had been derived from eggs or nymphs stolen from another colony—especially if we consider the great size of the C colony, as described above.

b On July 11th, 1904, a nymph previously introduced into nest C chanced to hatch in nest C3. Miss Fielde left her among the C3's for seven days, and then isolated her in a cell with some larvæ. Hence it is clear that this young ant knew no odour but her own, that of workers at least three years old, and that of a queen. A day or two after her separation Miss Fielde introduced one by one, in the manner described above, all the C1's, removing each of them as soon as a decisive reaction took place, and intercalating a period of rest between all the visits. The isolated young ant affiliated with the first, third, fourth, sixth, seventh, eighth, tenth and eleventh, but attacked the second, fifth and ninth.

In the same way, Miss Fielde then presented the C2's to the same ant. She affiliated with the first, third, fourth, fifth, seventh, ninth and twelfth, but attacked the second,

sixth, eighth, tenth and eleventh. She did not attack the C2 queen, but this queen avoided her so persistently that it was impossible to pass a definite judgment.

c A young ant hatched on July 11th, 1904, in the C2 nest, whose inhabitants were two years old, was submitted to the following test: She was left in the C2 nest for seven days, and then isolated for a day and entrusted with the care of some larvæ. Some C3 ☿, none of which were more than three years old, were brought into her cell. She affiliated with the second, fourth, fifth, eighth, eleventh and twelfth, but attacked the first, third, sixth, seventh, ninth and tenth. Miss Fielde then introduced some C1 ants, which were one year old. She affiliated with the first, second, third, seventh, eighth, ninth, tenth and twelfth of her visitors, but attacked the sixth and eleventh.

A similar experiment with a C1 ant was spoilt by a mistake.

If we suppose that the ☿ cannot reproduce colonies, and that the queens always preserve their own odours, how are fertile ♀ of different odours produced through workers which change their odour as they grow older?

In 1901, Miss Fielde separated a number of winged ♀ from the C colony, putting some together with ♂ which were their brothers from the same colony and others with ♂ from alien colonies. She supposed that the winged ♀ taken in the nest before their aerial nuptials were all virgins, and believed that she would be able to prove the affiliation of the progeny of sister-queens by the eggs which issued from them without taking the paternal influence into consideration. But she later realized that virgin ♀ often mate in their own homes, before they come forth, and that neither the possession of wings nor early capture could guarantee the virginity of a ♀; it could only be guaranteed by the sequestration of the ♀

nymph before she was hatched. For instance, Miss Fielde once saw some *Lasius latipes* ♀ which had been taken from the wild nest before swarming, drop their wings and lay eggs. She then observed that the queens in her artificial nests persistently avoided the kings of alien colonies, manifestly preferring those of their own colony. Mating in captivity, in artificial nests, is not uncommon, and must also be frequent in natural nests before the swarm.

We know that the eggs laid by ☿ often produce sturdy ♂. It is probable that such a ♂ communicates to the fertilized eggs of the ♀ with which he mates something of the odour possessed by his ☿ mother at the age when she laid the egg which produced him. This may account for the difference in odours among the progeny of sister queens, and the accumulation of such differences may explain the difference between the odours of various ♀ of the same species and variety. When a ♀ remains in the maternal nest after mating there, and rears her brood in the same place, the odours of this brood must become more mixed than those of the C Colony described above. The ♀ already fertilized which set out from the maternal nests found new colonies; the odour of the virgin ♀ produced here would depend on the age of the workers who were mothers of kings hatched in the season in which their founder-queens mated. In short, then, the *primordial* (innate) hostility between ants of different formicaries follows from two causes, combined in all possible degrees; *a* the difference in the maternal and paternal lineage; *b* the difference in age of the ☿. But neither of these causes of hostility is insuperable, as is proved by the alliances between young ☿, even those belonging to different subfamilies, and forced alliances between adults.

Besides the aura of her nest and other local scents, including that of her own track, an ant discerns yet other

odours; (1) Those which are incurred incidentally under certain conditions and which fade away in course of time; (2) the inherited odour of their mother, communicated to the eggs, larvæ, nymphs and young, newly-hatched ants, probably reinforced by the ontogenetic growth of the progeny after the egg-stage; (3) the progressive change of odour in the ♀, according to age; (4) the specific odour which characterizes the tribe, species, variety, etc. If to these various perceptions we add the recognition of familiar odours after months and years of separation, we must agree with Miss Fielde that ants are very well equipped for life in their little social world. If they lack reason and imagination, they possess at least the necessary basis of these two faculties: the knowledge of past experiences.

I have shown you here, friend reader, the significance of the most important experimental work of Miss Adèle Fielde. You may not be prepared to admit all these last hypotheses of hers, and you are at liberty to criticize some of their details, but you must needs join me in admiring her perseverance and exactitude, her highly conscientious methods, and the clear and acute judgment she displayed. This alone should convince you, if you were ever in doubt, of the desirability of votes for women! Even though there are many human imbeciles in both sexes, and though genius is rare on the whole, the male has no monopoly therein. Think of the ants and throw away your pride. Let us now consider Miss Fielde's other work.

4 The Communal Life of Ants (1905)

Here a few preliminary remarks are necessary. The odour of the nest is perceived by ants through the air, but the individual odour or savour of other ants, whether friends or enemies, is only distinguishable by the immediate

application of the nose, or in other words the antennæ, to the body of the ant which is being examined. Ants have two identical antennæ, and one alone of these may normally suffice for making the meticulous distinctions described above.

Two friendly species, *A. fulva* and *C. pennsylvanicus*, were separated for seven months, after which their respective odours had become so unlike that every time one of these old friends visited the others she was violently attacked. But when Miss Fielde introduced into either group an ant of the same species and age, derived from the same mother as her old associates of the mixed colony, she was always received at once with every sign of friendship, despite a long separation which, as we have seen in the case of *A. fulva*, may have lasted for three years.

5 Various Special Phenomena in the Life of Ants (1907)

Experiments must be prolonged for weeks and even months. Certain sister ♀ of *Camponotus pennsylvanicus*, which had been separated all their lives into one group of young ants and one group a year older, were induced so gradually and cautiously to form an alliance that Miss Fielde thought the young ones were absolutely reconciled to the odour of their elders. But just when the family union seemed to be complete, one of the elders would occasionally be killed by a younger one and a succession of conflicts would destroy the colony within three months.

On several occasions, Miss Fielde has made similar observations with groups possessing heterogeneous odours. One day, however, she introduced several ♂ into an artificial nest peopled with virgin workers of *Camponotus herculeanus*. The encounter assumed the appearance of an

attack by the ☿, but the ♂ were none the worse for it, and Miss Fielde soon saw that the apparent violence of the ☿ was caused by attraction, not antipathy.

In the life of ants there are numbers of factors whose influence must be carefully calculated if we wish to determine the cause of their actions. These include among others: (1) the presence of the brood; (2) the extent to which the nest-aura has been established; (3) domestic conditions in general; (4) the ants' familiarity with their immediate environment; (5) incurred odours; (6) inherited odour; (7) this odour progressively modified according to age; (8) specific odour; (9) the sensibility of ants to one predominating odour and the resulting encouragement or discouragement; (10) the ants' power of concentrating upon the object of their immediate interest and forgetting temporarily (by anecphoria!) all other matters; (11) finally, their memory by ecphory of old associations of engrams connected with their former experiences (see Semon, Vol I, page xliii and Vol II, page 4).

6 The Sense of Smell in Different Segments of the Antenna (1915)

Between 1900 and 1907, Miss Fielde made a series of long and patient surgical experiments upon *Aphænogaster fulva* ☿, removing one after the other the last seven segments of the funicle, which possesses eleven in all. She declares that she did not utilize for her experiments any ant which had not manifestly recovered after the operation, and sums up her results as follows:

The activity of ants is, as we have seen, guided by different odours, each of which is localized to some extent in five groups of the seven last joints of the funicle; Miss Fielde calls each of these five groups a 'sub-nose.' Here are her conclusions:—

1 The odour of the domicile or nest-aura, a mixture of the odours of all the inhabitants, is discerned through the air by the last segment of the antenna. By means of this odour the enemy terrifies and the friend attracts. When deprived of this distal segment she remains fearlessly in the home of the enemy until she pays for her unconscious temerity with her life.

2 We know that ants of the same species but different formicaries will usually destroy each other, although they sometimes rear the brood which they steal from their enemies. This colony odour, as we have said, depends on the age of the ☿; it is discerned by the last segment but one of the antenna. When this is removed, together with the last joint, ants of various formicaries live in complete accord, despite the mutual touch of their antennæ, which now alone guides their topochemical smell.

3 When an ant comes away from her home, she leaves on her path a *topochemical trail* which orientates her as she returns (see Vol. II, Chapters I and II). She recognizes her own odour (and, in my opinion, that of the objects which she touches) with the antepenultimate segment of the antenna, either by contact or through the air. As soon as this is eliminated, she is incapable of finding her scent again and loses her bearing altogether. The trail remains, but the ant can no longer follow it by smell.

4 The next joints, the eighth and ninth of the antenna, which in *A. fulva* are the seventh and eighth of the funicle, still distinguish the odour of the queen and the undeveloped young ordinarily her progeny. When they are removed, a ☿ which has hitherto tended her brood and her mother ceases to do so, and becomes absolutely indifferent.

5 Lastly, the sixth and seventh joints of the antenna, that is, the fifth and sixth of the funicle, discern the specific

odour. When these are removed, the most dissimilar species and sub-families will immediately intermingle without fighting. They even regurgitate honey-dew to each other from their crops. In this way, Miss Fielde was able to combine five different genera in close fellowship. Except for the regurgitation, this last experiment resembles the one I myself made in 1874 with ants whose two antennæ I had eliminated altogether (Part II).

With regard to ants whose antennæ are differently formed from those of *A. fulva*, Miss Fielde adds, among others, those which have only four or five joints to the funicle—careful observations at a later date will doubtless reveal olfactory functions in other segments, other 'sub-noses.' It is nevertheless certain that the scape and, in *A. fulva*, segments one to four of the funicle, do not distinguish odours discerned by the seven last joints. Miss Fielde thinks that the antennæ must be lubricated by the secretion of certain glands in order to perceive odours so well, and suggests that this may perhaps be the function of the champagne-cork organs (Part I, Chapter IV).

In conclusion, Miss Fielde defends herself against the objections of McIndoo, and, to some extent, against those of Wheeler. McIndoo denies that the antennæ are the organs of smell. He is wrong, as you will see by reference to Part II, Chapter I. We will now pass on to a criticism of Miss Fielde's observations and hypotheses.

7 Criticism of Miss Fielde

In my anxiety to remain just and objective, I have considered it my duty to put before my readers the results of the fine and patient experiments of Miss Fielde just as they stand. But that does not mean that I accept all her hypotheses and deductions. The future must judge. I agree to

Battle between ants of the same species (*Formica pratensis*).

Vol. II. Pl. X.

Petite pelouse entre deux arbres de la même espèce (Lawsonia humilis).

a great extent with the objections which Wheeler has lodged against her, the first of which is obvious: Miss Fielde was absolutely unable to remove the sixth, seventh and eighth joints, etc., of the antennæ without at the same time removing the last, and this fact alone makes it impossible to prove absolutely the localization of 'sub-noses' in five groups. All that is in our power is a relative localization by successive eliminations. This should have been emphasized.

In the second place, a glance at figure 23 (Part I) showing a whole antenna as viewed under a magnifying-glass, makes it plain that two or three varieties of topochemical nerve-terminations are intermingled equally on all the terminal segments of the funicle, and show no localization. Here, however, I must speak in defence of Miss Fielde; colours are not localized by our retina—and yet we do localize them. Moreover, it would seem that the 'organ of Corti' in our ear localizes the pitch of the sounds which we hear, but it does not therefore localize words, nor other specialities of hearing. And we are quite able to distinguish heat by touch, though the organs which communicate both these sensations to us are intermingled in our skin. The relative localization of a function is not necessarily connected with that of its sensory organs in all their details.

On the other hand, Miss Fielde claims that in five years she has not found in the antennæ of ants any other sense than a chemical one; Wheeler therefore rightly objects that she has completely ignored the tactile hairs of the scape and the base of the funicle. But from another point of view, the proof that these hairs are tactile can only be provided by analogy with certain hairs of other parts of the body, whereas topochemical smell dominates all the antennal activities of ants. Hence this polemic is not very conclusive. Miss Fielde certainly declares that an ant which had been in a

Petri dish for a year behaved as though perfectly at home in another cell of exactly the same nature. Wheeler rightly observes that recognition of this kind would probably be mechanical rather than chemical. Personally I think that Miss Fielde is somewhat too intolerant and absolute. She takes too little notice of differences in sight and touch according to sex and species, and she is a little too inclined to generalize. For instance, it is certain that although some ants are very warlike, others, such as *Myrmecina graminicola*, are very peaceable. Different colonies of *Formica exsecta* and *pressilabris* scarcely ever fight one another, and those of *Formicoxenus* have never been seen at war. True, both of these live in extensive polycalic colonies, which must have very mixed odours, and Miss Fielde thinks that these must render them more liberal-minded and consequently more peaceable. The large *Camponotus*, on the other hand, are generally as warlike as they are intolerant, and I once proved that a short separation of a few weeks is enough to destroy the power of recognition in ☿ of the same *C. ligniperdus* colony. All these facts have to be considered as a check upon over-hasty interpretations. The duration of memory may also vary according to species.

However that may be, such criticism of details does not detract a whit from the value of Miss Fielde's magnificent experiments, or from the additional depth which she has given to our knowledge. Her experiments should be continued by young myrmecologists—especially those concerned with successive amputations of the last funicular segments and the consequences they entail. It was Miss Fielde's own desire that this should be done.

Chapter III

ORDINARY WARS AMONG ANTS

When I was at school, they used to stuff our brains with the wars of Julius Cæsar and the learning of Greek verse from the Iliad, instead of teaching us to do free work in art and scientific observation, by induction and personal intuition. In those days my interest in ant-wars moved me to devote to them an epic which I entitled 'La Myrmécade'; but as I was entirely without the poetic gift, I soon perceived the triteness of my work; it was but a wretched plagiarism from Homer, and I put it in the waste-paper basket without finishing it. My epic described a war between some *Formica pratensis* and some *Formica sanguinea*, and indeed, a poet knowing as much about ants as Mæterlinck knows about bees might do well to take up my childish idea. I must request my readers to look at Plate I, which represents a war between two *Formica pratensis* colonies, and Plate II, which depicts another between this species and some *Tetramorium cæspitum*, both drawn from nature by Heinrich, who watched the wars which I instigated in order that I might have them illustrated. In addition to the two *Formica pratensis* ☿ shown at the bottom and on the left of Plate I, the reader should imagine those which are gripping one another with their mandibles and curling up their abdomens, and with his mind's eye watch them bespattering one another with poison as the *Formica pratensis* of Plate III

is doing to a man some distance away. He will then have the whole reality in front of him, and in a few moments the two combatants will be but a pair of corpses, still shining with the liquid poison which has just covered them.

Why is it that such fundamentally social creatures as ants should be guilty of such terrible wars between various formicaries? The reply has been given by Miss Fielde and myself in the two previous chapters. But this reply contains a contradiction in itself; why should different topochemical odours suffice to bring about war, when different species and even different sub-families may form alliances among themselves? Why then should the selection and mutations of phylogeny have tended to create differences in odours which bring about wars between creatures so capable of peaceful social alliances? I frankly admit that this question, which touches upon metaphysics, sends me off into a brown study for a while. If things were not as they are, in principle there would be nothing to prevent a 'universal formicity.' But if ants lived in peace with one another, what would they feed upon? They would be obliged to limit their reproduction by eugenics, and would moreover be continually forced to kill other animals and exploit their cattle in order to live. Let us own outright that we had better relapse into silence here than build up vain hypotheses; better bow our heads to fact than argue as to its 'why.' We must be content to state that neither sheep, nor swallows, nor cock-chafers, nor bees are free from mutual warfare, and that the termites are very rarely so—like our phylogenetic cousins, the apes.

1 Defensive and Offensive Wars. As I pointed out in 1874, the warlike 'virtues' of ants vary according to three principles:

a specific peculiarities. These are all the transitions imaginable between the most valiant of ants, *Polyergus*

rufescens, which knows no fear and seeks no retreat, even when alone in the midst of thousands of enemies, and its opposite extreme, *Formicoxenus* and *Myrmecina*, which I have never seen fighting, either singly or in defence of the colony.

b THE POPULATION OF A FORMICARY. The greater the number of inhabitants, the more enterprising and aggressive they become. The handful of small ☿ in an incipient formicary are generally very timid, and will hide and block up their nest-opening.

c STRAYING. As a general rule, when an ant strays a long way from her nest, her courage diminishes in direct ratio to the distance separating her from this nest and her companions; conversely, it increases at the same rate as the ant comes nearer again to her companions and her dwelling.

We cannot therefore judge them accurately without considering the three above factors in their numerous combinations.

True wars of defence are invariably wars of the weak against the strong; here I am not speaking of human hypocrites and their preventive wars which are supposed to be defensive. When it is possible to mobilize an armed force, the most common defensive measures on which ants rely are their hard, tough carapace, rapid flight, the faculty of 'shamming dead' by folding up their legs, a very secluded position for the nest and the obstruction of its doors by earth or other materials. Apart from these, most ants have one or several ☿ to guard the doors of the nest with their mandibles and defend it against any individual or collective assault. In Part V we shall encounter a special adaptation of the ♀ door-keepers for this purpose. We have seen *Formica rufa* and her kindred close their doors in the evening and open them in the morning with wooden materials; other species do the same thing in a different way, always for

purposes of defence. Colour-mimicry in the porters or in the whole nest will sometimes serve for defence. For instance, the colour of the nest of certain *Polyrhachis* of Java is a life-like imitation of a lichen which abounds on the tree it inhabits. The underside of a stone, or the bark of trees, also partially protects the dwelling of many ants against their enemies.

In this connection I must not forget *Azteca hypophylla*, which makes a cover for her little nest by connecting the bark of a tree, by means of a little carton, with the leaves of a climbing plant which leans against it.

But the great question at issue is how to live and feed the young, and there are various ways in which weak ants can tackle this problem. Those blest with great agility climb on to grass-stems, and even hunt for the corpses of large and stronger ones in the immediate vicinity of their dome, if not actually on it—especially when the two species are at war. They accomplish marvellous acrobatic feats in transporting these corpses, or even half-dead ants, from one blade of grass to the other, without touching the ground, until they are in safety. Some which are very small creep on the ground or the sand, in among the others, and as soon as the large ones show any sign of having perceived them, they feign death and so achieve the same result. They behave in the same way on trees and near aphids which are free, not enclosed, and also near flowers whose nectaries tempt them, decamping directly they are threatened by a stronger ant or the members of a more thickly-populated formicary. Then, too, they sometimes lay hold of the corpses of insects or small animals weaker than themselves. In short, they behave like simple thieves on the highways and by-ways, though they have as much right to all that they steal as the strong ants; for you must remember, dear

reader, the so-called right of *individual* property is not recognized among the ant-folk.

Weak and slow-moving ants which are provided with a hard carapace, like *Myrmecina*, *Proceratium*, *Alfaria*, *Sericomyrmex*, etc., solve the problem by living underground, beneath stones or in rotten wood, in small hidden nests, whence they come out in search of corpses, etc., trusting to the hardness of their skin and feigning death when other ants squeeze them vainly between their mandibles.

Offensive wars are the business of large formicaries of certain species which are particularly daring and combative. Their purpose is to conquer the means of subsistence by violence and extend forcibly the collective domain of the formicary. In contrast to the weak ants which own nothing but their small, hidden nests, the ants which feel that they are strong arrogate to their formicary the right of collective ownership, and so long as they prosper, they strive to extend this right further and further. This is especially true of independent polycalic colonies. In short-sighted ants such as *Lasius flavus* this ownership extends to the aphids through subterranean passages, and in certain *Dorylinæ* it covers their provisional hunting-ground. But in the outer world, among ants with comparatively good sight, collective ownership is represented by a portion of a meadow, a tree or several trees, a wood or even a stretch of sand. A strong colony tries to enlarge its domain at its neighbour's expense—to reach their meadows, their trees, etc. This is the source of wars. There is a great deal of amusement to be obtained in watching the skirmishes which precede wars of this kind. A colony which feels at home on a tree seeks to attack all strangers from the vantage-point. Feeble robbers, as we said before, can only creep and intrude and evade. Individually, the strong ones begin in the same way, but as

their numbers increase, they grow gradually stronger and stronger and show more spirit. And thus it happens that a tree on which aphids have settled, for instance, may become the pretext for a spontaneous war-epic, such as I once observed at Vaux between two kinds of *Formica pratensis* colonies. But as in the wars of men, the result is not always as we should desire it. If the two formicaries are approximately equal in strength, they exterminate each other without any definite result, and the third thief which benefits by it all is a tribe of small, weak ants, which can then bear away corpses from the battlefield as we have explained before, frequently the same night, as food for themselves and their brood; this I have often seen them doing. In these cases, as the two sides grow weaker they eventually realize the fruitlessness of their efforts, after which they lose heart and gradually end their war, which may have lasted for several days, by a truce which enacts that each shall studiously avoid the frontiers of the other's domain. However, ants are like men; despite their memory for odours, they often forget the lessons of the past, and in the following year the war begins again.

The loss of a tree infested with aphids is one cause of progressive degeneration in a colony and the permanent loss of its spirit. We have already mentioned this sudden loss of spirit among ants which have been put to flight in war as a psychological phenomenon of feeling. Under these circumstances, they are seen to abandon their nest and even their precious brood. In short, wars on a large scale often do colonies more harm than good, whereas easy triumphs over much weaker colonies add to their strength.

2 The Weapons of Ants. The weapons used by ants vary almost as much as their species, and we must

understand their nature in order to understand these wars. Chief among them are the following:

The *agility* of our friends is often incredible, and will make a terrible foe of a small ant with a weak covering of chitin, which can be killed with a single pinch of the mandibles. The long legs of these creatures enable them to dart like arrows, so that nothing can be seen of them but streaks flying without wings in every direction. This description applies to *Prenolepis longicornis*, *Iridomyrmex humilis*, *Machæromyrma bombycina*, *Acantholepis gracilicornis*, and other species. The agility of these ants renders them extremely daring and aggressive, for the other species are incapable of reaching them. Thus I have seen *Pr. longicornis* reigning like a queen over the lanes and roads of the island of St. Thomas, as she does in the hot-houses of Paris, and as *M. bombycina* (see Plate I, Part V) does over the dunes of Biskra in Algeria. But there are ants less prone to running away, such as *Tapinoma*, *Azteca*, *Cataglyphis*, our *Serviformica picea*, etc., whose agility is none the less so great as to be one of their principal weapons.

The second great weapon of all ants consists of the *mandibles*. Fig. 3, Part I, has given us an idea of some of the shapes they may assume. Plate III shows us the mandibles used for piercing the heads of other ants; finally, figs. 106*B* and *C* show us directly how they achieve this purpose. We have seen how the mandibles of *Odontomachinæ* (fig. 3*E*) are utilized, not only for pinching but for threatening and leaping, and how *Acanthognathus* has two kinds of mandibles, one short, for carrying, the other long for defence. The harvesting ants, *Messor*, *Holcomyrmex*, etc., as well as the *Pheidole* ♀, use their mandibles not only to cut up seeds or prey, but also to bite and slay their enemies. Ants with sharp mandibles cut leaves and also the bodies of species

which they fight. Ordinary mandibles with dentate terminal edges, used for carrying, sawing and building, may also crush small enemies and saw off the heads of large ones; small ants use them for clutching hold of big ones by the legs and antennæ, as the big ones also do to each other. This process can be plainly seen in Plates I and II. Certain curved mandibles belonging to the ♃ of *Eciton*, etc. (fig. 3, Part I) are used against mammals rather than ants.

The sting, with its pricking function, together with the poison it ejects, is the most formidable weapon of the *Ponerinæ* and many *Myrmicinæ*. But it has no effect upon ants unless it is capable of reaching the soft parts. It is powerless against the hard, spine-covered carapace of *Cephalotes atratus*, for example, which *Eciton* attacks in vain in Venezuela. Some European *Neomyrma rubida*, on the other hand, killed within one hour all the *Formica pratensis* which I heaped up on their nest. In order to wield its sting, an ant seizes her enemy by a limb, which she uses as a support, and then curls her abdomen round it and seeks a vulnerable place on the creature's body, wherein to insert the sting.

In the *Formicinæ* the sting is replaced by a poison-squirt from the anal vesicle, as shown in Plate III. A douche (Plate I below) of the formic acid contained in the poison often suffices to kill the enemy. The ant seizes the latter how and where she can, curls her abdomen round it and sprinkles any haphazard part of its body with formic acid. But whereas the *Formica*, especially those of the *rufa* group, use and abuse their poison in their combats, *Camponotus*, *Lasius*, *Prenolepis*, etc., do so to a much less extent. ☿ of the subgenus *Myrmobrachys* of *Camponotus*, on the other hand, rear themselves up on their back legs and shoot out their

poison some distance away, as *Formica rufa* does. I myself have observed this in the case of *M. zoc* in Trinidad.

In the *Dolichoderinæ* (except for *Aneuretus*) and many *Myrmicinæ*, the poison vessel and the sting are atrophied to such an extent that they have ceased to be of any use. In the *Dolichoderinæ* they have been replaced by anal glands whose poison is a terrible instrument of war, especially for defensive purposes. Fig. 97 shows how *Tapinoma erraticum* uses it to put a little *F. pratensis* ☿ out of action, but she often does the same thing to the large species. As soon as this poison comes out of the anal vesicle, it gives forth a strong aromatic odour and begins to effervesce, and is presently transformed into a resinous matter. This sticks to the antennæ and accordingly destroys the topochemical smell in the enemy at which the *Tapinoma* directs it. For this purpose, the abdomen of most of the *Dolichoderinæ*, moved by a petiole which is almost scaleless or whose scales are much depressed, is extraordinarily mobile in every direction, and has an inimitable way of twisting about. *Iridomyrmex*, *Azteca*, *Liometopum*, etc., put their most terrible enemies to flight by this means. I myself have seen *Eciton Burchelli* withdraw before some *Azteca* which were making passes at her with

Fig. 97

their abdomens. While discussing the parasitic ant *Bothriomyrmex merionalis*, whose anal gland can be seen in fig. 22, Part I, we remarked (Part III, Chapter II) how injurious its anal poison is to other ants, though it gives out no odour.

The sting of the *Dorylinæ* tends to be weak, and for offensive purposes, therefore, they chiefly depend on their numbers, their courage and their mandibles. Other ants, such as *Oxyopomyrmex*, according to Santschi, have special secretions which frighten their enemies. Still others, such as *Dendrolasius fuliginosus* and other *Lasius*, emit a repulsive odour, which also seems to harm their adversaries. Hence not only are ants well equipped by their senses, as Miss Fielde says, especially by their sense of smell, but also by their arms.

3 Wars Between Enemies of the Same Species. Desirous as I was of witnessing the epic deeds of which I had dreamed in my childhood, one fine spring day I grew weary of waiting for a war to arise spontaneously, and deliberately brought it to pass. In such weather ants sleep all night long and crowd together in the morning above their nest, so that it is easy to put them all into a bag together. I was not satisfied with the Trojan inhabitants of nest *X*, nor the Greek population of nest *Y*, but chose to add a third camp, full of Persians, which I will call *Z*. The Iliad, or rather Myrmecad, gained in tragic interest on this account. The three camps consisted of different colonies of *Formica pratensis*. I must mention that as the fighting tactics of ants belonging to the same species are instinctive, they are always the same on both or on all three sides, and this is an important point to remember.

Nest *X*, whose inhabitants were slightly smaller than those of *Y* and *Z*, stood on a sloping piece of turf. I poured a bag full of the *Y*'s about 1 metre to the left of nest *X* and

another full of *Z*'s in the shade of a bush about 3 metres to the right of the same nest. As yet none of them had any brood.

It was early morning, before 8 o'clock. The *Y*'s, having recovered from the shock of being gathered and turned out of the bag, remained on their mound, put it in good order facing the sun, and scarcely ventured away from it, while the *X*'s opened their doors and began to run out on to one of their exposed paths which lay in the direction of the *Y*'s. So they strayed unsuspectingly, one by one, into the midst of the *Y*'s and were seized upon, drenched with poison and slaughtered; and it was more than half an hour before they could give the alarm. A thick tuft of grass separating them from the *Y*'s mound also made it somewhat difficult for them to return.

The *Y*'s gradually became excited; a considerable number of their ☿ went to see what was happening on the right and came within 2 decimetres of nest *X*, some of whose stragglers had at last succeeded in escaping and had gone back to give the alarm to their formicary. A number of *X* ☿, which had hitherto been warming themselves peacefully in the sun, then set out on the march and took possession of the tuft of grass and its neighbourhood. Several fights took place, mainly among scattered groups, but they were sharp enough to alarm the *Y*'s, which were all on the alert, having been wakened by their journey in the bag. They accordingly formed a close column, marched to the left of their nest, released their companions and captured the *X* ☿, which they dragged back to their mound and slew. At this juncture the alarm became general in the camp of the *X*'s, which ran in close ranks through the tuft of grass and 2 decimetres farther to the left, where they formed a complete battle-front at half-past eight and did not shift their

position until half-past nine. There was a steady increase in the number of reinforcements, and also in the violence of the battle. Though the Trojans were the smaller of the two forces, they were capable of putting up a good defence.

Compared with the fighting between *F. sanguinea* and *pratensis*, this battle displayed an almost pedantic regularity: a single front, 1 decimetre broad, on which strength and numbers were the all-decisive factors. Chains of from three to seven ants were formed, like those seen in Plate X, but much closer, especially on the ground. The individuals in these chains clung to the ground and made extraordinary efforts to drag each other into their own camps. At the same time, all the ☿ which could manage to curl their abdomens drenched their adversaries with poison. As Huber says, sometimes in the heat of the battle we see a ☿ make a mistake and bite a companion instead of an enemy; but she nearly always realizes her error in time, thanks to her antennæ, and lets her friend go before she uses her poison. Very occasionally, however, in multiple battles, accidents will occur simply through clumsiness. In that case, the companion pays her back in her own coin, and the enemy takes advantage of the fact to drag the two unfortunates half-dead to her camp, where we can picture their end. Plate X shows some *F. pratensis* seizing hold of each other by the mandibles, legs and antennæ, but sometimes they also take hold of their enemies by the head, thorax or petiole. Many a time have I seen large *pratensis* ☿ crush the head or thorax of a small enemy ☿ with a single stroke of their mandibles. At the top of Plate X we may also see the preliminary threats offered before the fight by an *Achilles* and a *Hector*, and two corpses at one side of them.

Nevertheless, by dragging all the chains gradually along,

with them, the *Y*'s were managing to gain the upper hand, while the *X*'s took few prisoners: they went on working peacefully on their dome, however, as though nothing had happened. I even saw a few ☿ which were setting out for the fray stop for a few seconds—not more—to taste some tempting honey which I, the Satan of the epic, had set in their way. About half-past nine, the *Y*'s made a heroic dash and broke the front of the *X*'s, forcing them to retreat for a decimetre and a half, to a spot 5 centimetres to the left of the grass-tuft. Here a plant, a dry leaf and a little fallen twig offered the *X*'s a rampart and checked their retreat. But now a lamentable panic overtook the camp of the *X*'s. On their dome I saw ☿ cross one another's paths in all directions, with two or three sharp, jerky blows of the antennæ, their mandibles half-open the while. For a moment I thought they were going to escape altogether, but instead of this, the whole formicary was aroused by the general alarm, and hosts of warriors surged out through every door to save their native land from the invader. They widened the battle-front on both sides and outflanked the *Y*'s. The latter had taken hundreds of prisoners, after concentrating all their strength on the field, but were unable to break through the last line of the *X*'s. The battle then waxed fierce; 3 square centimetres of land were literally covered with chains of ants pressing one against the other and struggling with the fury of despair.

At about half-past ten, the front of the leaf and the dry twig became untenable for the *Y*'s, which were overwhelmed on all sides. Despite their efforts, they in their turn were obliged to retire to the old front they had held at half-past eight; but they were unable to maintain this position. The unwearying *X*'s continued to advance, in spite of the fierce resistance of their enemies, which lasted till 11 o'clock. By midday the *X*'s had reached the edge of the *Y* mound,

and their enemies, seized with a general panic, fled in disorder about the meadow. The Trojans had vanquished the Greeks. But the *X*'s did not pursue the enemy, and we shall see why.

All this time the *Z*'s had remained in the shade of their bush—the more calmly since the *X*'s, being over-concerned with their left, had deserted the right. Then Satan (represented by my humble self) sowed discord by gathering the *Z*'s nearer and placing a few fragments of their mound in the direction of nest *X*, so that by about 11 o'clock a few fights were taking place some 2 decimetres away from nest *X*. As soon as they had finished with the *Y*'s, the *X*'s turned upon the *Z*'s and began once more to wage violent war.

But since the *Z*'s on the one hand received no reinforcement, and the *X*'s on the other were weary of fighting, it soon came about that the *X*'s advanced no further than was necessary for defence, whereas at about 12-30 the *Z*'s began to retreat. Towards 3 o'clock in the afternoon they were evading each other rather than fighting, and the strife came to an end for want of combatants. After these two battles, hundreds of corpses covered both battlefields, especially that to the left of the *Y*'s.

Two days later, I placed an enormous handful of *X*'s on the provisional nest which the *Z*'s had dug out for themselves, and allowed them to besiege this fort. The *X* ☿ pulled nearly all the *Z* ☿ out of their nest and killed them in broad daylight; the few remaining *Z*'s, like the defeated *Y*'s, fled in distress to settle farther off and found small nests for themselves. The epic was at an end; the Trojans had vanquished both Greeks and Persians, and Satan was satisfied. In conclusion, we may note that the *F. pratensis*, unlike the *F. sanguinea*, continued to wreak their fury upon their

half-dead enemies, even when they could no longer move anything but the ends of their tarsi.

Different formicaries of *Tetramorium cæspitum* will break out at any moment into spontaneous battles; I have even observed this in those towns of the United States to which European *T. cæspitum* have been imported. At Zurich in 1870 I even observed a battle of this kind extending over a piece of ground more than 30 metres long, at the edge of a grass-bank near the University. The sting played a great rôle in this battle; the ants curled their abdomens back one against the other, and thousands of dead bestrewed the ground. Three or four were seen to surround one other, and when they had been separated, this solitary one was found to be mutilated and half dead. These wars that I watched lasted for more than a month in springtime, and their intensity never slackened until they were nearly over. The nests are at the same time so common and so scattered between the paths and in the grass, that it is almost impossible to discern which region belongs to a particular community and which are their respective exit-holes. In 1872 I observed some hundreds of these conflicts in the suburbs of Vienna.

But sometimes they are not very serious conflicts, and the sting plays hardly any part in them; it may almost be questioned whether they are not more in the nature of games such as we have described in Part III, Chapter III. One day I saw 2 square centimetres covered over with a black mass of *T. cæspitum*, which were pulling at each others' legs and antennæ. None of them curled their abdomens, and there was no violent expenditure of effort. All the ☿ stood still and pulled in opposite directions. Nothing was in motion except the antennæ and the abdominal rings, which were moving upon one another—perhaps stridulating. I

made a single gesture to frighten these ants, and it had the effect of making them all relax their hold and flee, each to her own hole. None of them were dead, and only a few ☿ were suffering from a scarcely perceptible limp. I have witnessed all kinds of transitions between affairs of this kind and battles such as the one quoted above from my observations of 1870. Working on the lines suggested by Miss Fielde, there should be material here for the study of odours.

I also observed a fierce spontaneous conflict between two colonies of *Myrmica lævinodis*, in which the sting came into action.

In the Swiss Alps I came on the scene of a spontaneous fight between two colonies of *Camponotus herculeanus*. The one colony *O* inhabited the interior of the enormous hollow trunk of a dead larch. The ants poured out of their nests in hundreds and ran wildly in all directions, knocking the trunk with their abdomens and striking each other on the forehead. The noise was distinctly perceptible to my ears. The ants ran to the foot of the trunk, where the enemy *P* was waiting, having, apparently, come from a wood situated on the other side of the road, which a few of their stragglers were still crossing. The *P*'s appeared to be the aggressors, but they were repulsed with loss by the *O*'s. However, I saw one *O* ☿ spring impetuously at a *P* ☿ and let her go without being able to bite her. The two combatants often seized each other by the body and rolled on the ground, and often one of them would emerge from the encounter in a mutilated condition or half cut in two. The *O*'s, being more numerous, were reinforced, and the worker *P* was then torn in pieces. Others were simply beheaded. Strictly speaking, indeed, in the wars of the *Camponotus*, unlike that of the *Formica* and *Lasius*, the strong mandibles of the large ☿, moved by their powerful muscles, play a much more important rôle than

poison. This also accounts for the fact that enemy *Camponotus* rarely seize each other by the legs, since they are afraid of being beheaded or cloven in two.

Gounelle relates how *Camp.* (*Myrmobrachys*) *mus* of South America, when attacked, gives the alarm by striking violently on its nest of leaves, thus producing a noise very much like that of a rattle-snake. *Camponotus* (*Myrmothrix*) *Hannani*, which I myself discovered in Jamaica, behaves in a similar fashion inside its nest, partially constructed of carton.

As I said before, *Polyergus rufescens*, Huber's amazon or legionary ant, is the boldest of all, and never retreats before an enemy. As for her conduct towards enemies of her own species, we have the following information from Huber:

"I decided to use the ants in my apparatus for an experiment which I had long contemplated but always put off because I became attached to my prisoners. It was my intention to set two legionary armies against each other: with this aim in view, I waited until those of another mixed formicary situated in the garden were taking their departure, and I put the artificial formicary in front of their column.

After a little bickering, which took place at the door of the apparatus, the ants inside came out in full force, and the enemy column seemed to be desirous of avoiding the battle; first it changed its direction, then it retraced its steps and returned to its home. Several ants began to pursue it: some of them went as far as the enemy formicary, but were retained there; I only saw two or three escape and hurry back. The whole amazon army then came out, and moved in the direction of the mixed formicary. I expected a general engagement; but when the column was a few paces away from the entrance, it wheeled round and went back, except for a cluster consisting of about three hundred legionary ants, which continued their way until they reached

the formicary. Those at the surface seemed to be in a very excited condition, as though they had foreseen the attack which threatened them. When the little troop arrived, they fought each other hand to hand; but the strangers rushed into a gallery with such impetuosity that the others could not stay them. This bold incursion availed them nothing, for they all perished, though not before they had worked considerable havoc, for when the amazons of the natural colony began their expeditions again, I saw that their army was reduced to half what it had been before. The artificial formicary had not suffered such severe losses. I replaced it on the grass, and left the black colony free to emigrate, which they did in the same order as on other occasions."

Later on, in 1869, I repeated Huber's experiment with the amazons of my apparatus, which I set down near an enemy formicary at 4 o'clock on an August afternoon. The enemy army dared not come out. A group of *Polyergus* ran from my apparatus, and a terrible conflict followed. The enemy amazons seized each other by the thorax and bit furiously. They formed themselves into little knots of five or six, and rolled on the ground till it was impossible to distinguish individuals. My ants were all killed, but the bulk of the army did not come out. On the whole, therefore, I merely confirmed Huber's statements. Here again, the hooks of the mandibles were used to more effect than poison. In *Polyergus* the battle-fury sometimes becomes terrible; they snap right and left with their jaws and abandon all distinction between friend and foe. They are like mad creatures.

With regard to fighting between various *Formica sanguinea*, I must refer the reader to my remarks in Chapter I § 2 above, and similarly for *Leptothorax*. In these cases, alliances are more frequent in nature than wars.

As for the *Dolichoderinæ*, I have observed wars between different colonies of *Tapinoma* which fight very fiercely, but seem to receive less harm than other ants from the secretion of their anal glands. On March 29th, 1868, I had established a formicary *D* of this genus in a small glass-covered apparatus with frames, inside which was a little earth. The ☿ had here built some large chambers between the two glass walls, whence they departed in search of food, through the single exit-tube which communicated with the manger. On finding another formicary *E*, which was larger and contained stronger ☿, I took it as a whole and placed it in communication with the same apparatus by means of a plaster arena and the tube. A sharp fight began between *D* and *E*. The *D*'s had the worst of it, and being unable to flee to any other place, they withdrew into the apparatus, where they made a wall of earth in front of the *E*'s. Their enemies then ensconced themselves in the front part of the apparatus and accordingly remained in sole possession of the manger, which I restored after removing the arena, deserted by the *E*'s. Not caring to dig chambers for themselves, these *E*'s destroyed the wall of the *D*'s several times, and every breach was followed by a short combat in which a few *D*'s were dragged away and killed by the *E*'s, while their sisters hastened to repair the wall farther back with earth from the bottom of the apparatus.

This guerrilla warfare continued until May 7th, that is for a month and a half. At the end of this time, the *D*'s were all driven to bay at the bottom of the apparatus, and nothing was left to them but a last feeble earth wall. They had kept an unbroken fast all this time, but despite this none of them were dead, except the few ☿ killed by the *E*'s. They had even sustained their ♀, some of her eggs and a few larvæ at the expense of their own bodies, which had become remarkably

thin, in contrast to the large, well-filled abdomens of the *E*'s. On May 6th, I placed the apparatus in the sun, and several breaches were made, followed by fighting, but the *D*'s continued to repair the earth-wall. On the 7th their new position in the sun became untenable; one breach was made after another. Several *D*'s were dragged about and mauled by the *E*'s. When I returned from my university course, all was over; the *D* and *E* chambers were in communication, and all the ants were intermingled. Brawling had ceased, and the alliance was complete.

Four or five corpses, found in the manger that evening, alone bore witness to the final fray. The *E*'s regurgitated honey-dew to the *D*'s, and henceforth they lived in perfect harmony.

4 Wars Between Enemies of Different Species or Races. Here an enormous rôle is played by the way in which the *specific tactics* vary instinctively. The most interesting habits are those of *Formica sanguinea* when pitted against *F. pratensis*, whose manner of fighting with her own species has just been described. Instead of forming a battle-front, the *sanguinea* proceed by sudden surprise attacks. While the *pratensis* front advances in massed formation the *sanguinea* retreat, but they send out squads to make flanking movements against the *pratensis* front, and carry out sudden attacks on the flank or in the rear with incredible daring, thrusting their way amid the enemy, biting to right and left, but never running amok and injuring the ants thus thrown into confusion. Such tactics on the part of ants as large and strong as these sow disorder in the close ranks of the *pratensis*. Provided the *sanguinea* have only half their numbers, and are insistent in their attacks, the front of the *pratensis* grows visibly weaker, for they have wasted their strength and their time in wreaking vengeance on half-dead

enemies. The *sanguinea* have an uncanny way of recognizing any sign of hesitation or weakness on the part of their enemies, and as soon as they perceive these signs there is no limit to their daring. Each of them then springs single-handed into the midst of a surging host of *pratensis*, and delivers its blows with redoubled speed and insolence. Soon the *pratensis* are at the end of their resources, and overwhelmed with their growing despair, they know not what to do with their brood. But as soon as a *sanguinea* catches sight of a larva or cocoon, she snatches it at once from its bearer, which has no longer the courage to dispute it with her, even when the *sanguinea* is small and single-handed in the midst of a host of enemies whose discouragement she senses. Only when the *sanguinea* are too scattered or when the temperature is too low will the *pratensis* pin them to the ground and slaughter them. But when they feel that they are vanquished, the *sanguinea* retire in good order with their brood before the *F. pratensis*.

But the same tactics which render one species strong when face to face with another may render it weak when face to face with a third. We shall see the truth of this in the case of *P. rufescens* when matched with *F. sanguinea*.

In 1871 I observed a small spontaneous war between two different races of *Myrmica scabrinodis*, one small and pale and the other large and dark. The small ones, being more numerous, seized the dark ones by the legs and pinned them to the ground, where they tried to kill them with their stings and mandibles. But this species is very tough. The large ants were presently reinforced, and thereupon both sides formed chains and pulled at each other. One ☿ seized an enemy by the frontal grooves, and so uplifted her and bore her to her camp. As the dark ants eventually won the day, the small ones disappeared as though by magic into

the cracks in the ground, and blocked the little holes leading to their nest with grains of earth in such a thorough fashion that the dark ones were unable to follow them, and took their departure.

Wars between different *Camponotus* species closely resemble those described above as between two colonies of *C. herculeanus*. I provoked a fight between some *C. vagus* in a flask and some *C. ligniperdus* ensconced in a piece of wood which they had sculptured. A *Camponotus* frightens its adversary by a violent forward movement of the whole body, holding its antennæ down and pointing backward, and keeping its mandibles open and the position of its feet unchanged. The large ☿ which guard the doors of the nest behave in a similar fashion, rather like that of *Odontomachus*, but without afterwards leaping back so far. At the same time they rear up as high as possible on their front legs to avoid being seized from behind. If they manage to get hold of an enemy's body, they contract their solid mandibles with all their might to crush or decapitate it, curling their abdomens as they do so in order to pour their poison on the wounded place. When they seize each other by the mandibles, they soon let go, for this, except for the chance of using poison which it offers, is reckoned an unsuccessful attack. These are the tactics of the large ☿; the small ones keep behind, or sometimes they cling to one of their enemy's legs and are slain.

Despite their smaller numbers, the *vagus*, which were more robust than the *ligniperdus*, killed more victims than they. For instance, a large *vagus*, which had contrived to catch a big *ligniperdus* by the neck, squeezed it so tight that all the limbs of the enemy were convulsed, and its head rolled several centimetres away from its body. The *vagus* army gradually conquered the entire nest, and next

day they brought their larvæ thither and posted a large ☿ on guard before every opening. When I opened the flask, the *ligniperdus* were seized with panic, and ceased to defend themselves, but they carried their brood away and tried to climb on the glass. The *vagus* then fell upon them and bit them on every side, one little ☿ displaying special ferocity. A large *ligniperdus* was half decapitated and afflicted with convulsions, but she partially recovered, opened her mandibles, recognized her enemies, and, not perceiving the signal for retreat, went on biting entirely on her own account; she almost went so far as to seize a *vagus* by the neck, but two *vagus* captured her and pulled her in the opposite direction. The commissures of the ganglia between her head and thorax, already damaged, were now completely sundered, and she perished. Then followed a kind of truce, in which the foes showed their teeth at each other and separated without fighting. In the evening, I placed in the flask about ten big and somewhat darker *ligniperdus* from another colony; but they were attacked with one accord by the *vagus* and the first community of *ligniperdus*, and once more there were a few casualties. The first *ligniperdus* tried again to escape, but the *vagus* retained their mastery. Next day, however, I found the *vagus* army all torn to pieces by the united forces of the two *ligniperdus* colonies, which had ended by forming an alliance with each other. This time the specific odour had triumphed over that of general association. I kept my ants a few days longer to satisfy myself as to the stability of the alliance.

While discussing weapons, we have already pointed out the anal glands of the *Dolichoderinæ*, as shown in fig 97. When I set a crowd of *Tetramorium cæspitum* to attack a colony of *Tapinoma erraticum*, I could perceive nothing at first, except a mixture of the two species; but I soon

distinguished details, by means of my microscope. A *Tetramorium* would open her mandibles and threaten a *Tapinoma*, which immediately turned her abdomen to one side, towards the enemy's head, and sprayed it with an odorous liquid, bubbling and effervescent, from her anal vesicle. The *Tetramorium*, finding her antennæ impeded, drew back and rolled on the ground, rubbing and befouling her head in the soil. Sometimes she would even remain there as though dead after receiving the discharge. I saw one *Tapinoma* spray more than ten enemies, one after the other, without any effort; the one essential was that the end of her abdomen should touch the body of the *Tetramorium*. Nevertheless the *Tapinoma* were frightened by the number of their enemies, and probably also by the knowledge that the contents of their anal vesicles were diminishing, and all of a sudden they opened three of their nest-doors and fled in three close columns with their ♂, ♀, larvæ and nymphs. In a quarter of an hour's time, the whole colony had left the nest and sought another home, without incurring the death of a single ☿. The *Tetramorium* had profited too much by their experience to make any attempt at pursuing the *Tapinoma*.

F. sanguinea, like *F. pratensis*, often comes to blows with *Tapinoma*, but she is treated to a douche, as we have shown in fig. 97, and rarely manages to seize a *T. erraticum* and crush her between her mandibles.

The departure of the ♀ and ♂ of *Solenopsis fugax* in autumn to their aerial nuptials is often the starting-point of wars between this species and the ants with which it lives in lestobiosis.

I saw a violent combat which originated thus between some *Tetramorium* and *Solenopsis;* the latter, being more numerous, seemed to gain the upper hand. At other times, small groups of *Formica sanguinea* often amuse themselves

by hunting *Lasius niger* and *flavus*, killing their ☿ and stealing their cocoons, which they eat but never make into slaves.

Formica exsecta and *pressilabris* are predominantly peaceful and readily form alliances with other colonies. But in their wars with other *Formica* (*pratensis*, *sanguinea*), they have curious tactics, in keeping with the formation of their heads, which are deeply indented at the back and slightly elongated and flattened in front. They always march in close ranks, and never get far separated. But they are much more alert than *pratensis*, with which I have seen them in conflict. They leap to right and to left, constantly biting, as *sanguinea* does, but they would never at the outset wreak solitary vengeance on a foe. On the other hand, they would fling themselves two or three at a time at the legs and antennæ of a *pratensis*, and begin to drag her in the opposite direction. Presently another *exsecta* ☿ would climb nimbly on to the back of the enemy and seize her by the neck, which she squeezed with all her power between her mandibles, as shown in fig. 98, and sawed relentlessly away until the *pratensis* was thrown into convulsions and her head fell off. Meanwhile the *exsecta* which had grasped her by the legs had for the most part let go, and thus a number of *pratensis* could be seen carrying *exsecta* much smaller than themselves on their backs. One *exsecta* was not powerful enough to decapitate the largest *pratensis;* several were required for this purpose. However, if a *pratensis* catches hold of the body of an *exsecta*, she crushes it at once. I have sometimes even seen *exsecta* succeed

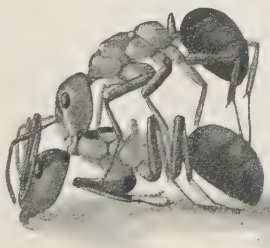


Fig. 98

in decapitating the ☿ of *Camponotus ligniperdus*. *F. pressilabris*, being smaller in stature and in numbers, scarcely ever fights any ants but those smaller than herself—*F. fusca*, *Lasius*, etc. They are terrified lest some enemy should seize them by the legs, as does *Lasius flavus*, for instance. *F. pressilabris* has elevated the decapitation of her enemies into a fine art. Some *exsecta* and *pressilabris* colonies which I once established at Vaux would engage in warlike campaigns against *Lasius*, *Formica* and even *Camponotus* of the neighbourhood, in order to steal from them bushes and stems infested with aphids. While in the garden of an hotel in Colombia, I observed a fierce fight taking place on a tree-trunk between one colony of *Monomorium Pharaonis* and another of *Cremastogaster Steinheili*. The first army used their stings by curling their abdomens underneath them, while the second curled their abdomens upward and poured poison from the tips. The point at issue between them was the bark of the tree. On the other hand, though there are an enormous number of *Monomorium Salomonis* colonies in Algeria and Tunis, quite close to those of various races of *Cremastogaster Auberti*, I have never seen a spontaneous battle between the two, or between different colonies of either species.

Dendrolasius fuliginosus is shunned and feared by all other ants for its enormous colonies, which are often polycalic, and likewise for its loathsome odour. It cultivates aphids, but is also carnivorous. I have seen it spontaneously plunder the nymphs of a *Myrmica* nest which it had invaded despite the stings of the defence-force. I once put the contents of ten *F. pratensis* colonies in front of one of the trees occupied by a polycalic colony of *D. fuliginosus*. When the *F. pratensis* first assailed them, the *Dendrolasius* passed on the antennal alarm to their other nests, situated near at hand in various trees of a thicket, from which thick black colums then poured

out and resolutely attacked the *pratensis*, causing great slaughter. The *pratensis* were thrown into a panic, and despite their numbers they fled, abandoning nearly all their cocoons, which the *Dendrolasius* eagerly bore to their trees and devoured. We do not know whether it is the poison of the *Dendrolasius* or their odorous secretion which is so harmful to other ants, but in any case they certainly could not kill so many *F. pratensis*, larger and more muscular than themselves, with their weak mandibles.

The habits of *Messor* will be discussed in Part V. These ants—especially the races and varieties of *M. barbarus*—make war on each other for the sake of stealing stocks of grain. Compared with other ants they are heavy and clumsy. For instance, certain *M. structor* were scarcely able to defend themselves against a cluster of little *Tetramorium cæspitum* which I had poured on to their nests, and several of them even allowed themselves to be dragged away and killed by this enemy.

The following interesting observations were made in the spring of 1918, after an extraordinarily dry winter at Braila in Roumania, not far from the mouths of the Danube, by my brother-in-law, Dr. Arthur Brauns, then an army doctor :—

"April 27th, 1918. During the hottest hours of the day, none of the *Messor* (speaking of *M. barbarus* r. *meriodionalis*) came out of their nest, while the *Cataglyphis* (speaking of *C. viaticus* r. *orientalis*) ran about in every direction. In summer *Messor* works by night and closes its doors by day with grains of earth, for there is no sand at Braila. On dry winter days, however, as well as in spring and autumn, they keep their doors open by day, opening and closing them every morning and evening. In the evening of the 27th, the rim of a craterless hole belonging to *Messor*, situated

on a piece of rising ground, was dotted with large and small ☿, waving their antennæ about and opening their mandibles. These belonged to the large, swift genus *Cataglyphis*, distinguished by its long legs and antennæ. They arrived singly from either side, but withdrew before the defenders of the nest, trying, however, to catch those which ventured out too far from the openings, and sometimes succeeding in capturing a small ☿. But this little creature would then put up so good a defence with her mandibles, and also with the poison of her abdomen, that the *Cataglyphis* would let her go. The courage with which a single *Cataglyphis* will spring upon such a formidable row of open mandibles is truly astounding, and evidently results from the confidence which these ants place in their agility, their relatively good sight and their adversaries' slowness. The *Cataglyphis* never make a co-ordinated attack. What is more, when it happens that two of their ☿ come together from two opposite directions above some hole in a *Messor* nest, they sometimes accidentally seize each other and roll over together for an instant, so entirely are they carried away by their battle-fury. Once I even saw a large *Cataglyphis* kill one of her little companions in this manner with a single snap of her teeth—needless to say, without intending to do so.

Once when three *Cataglyphis* happened to attack a *Messor* hole at the same moment, a *Messor* ♂ managed to escape from his friends, and strayed about like a lost thing, unable to find his way back to the nest. A *Cataglyphis* ☿ caught him, and after a weak and unavailing struggle, bore him away. Winged ♂ strove to get out of all the *Messor* holes, but strong ☿ came to the rescue and dragged them back into their nests by the legs.

May 19th. This was the swarming-day of the *Messor*. Many of their ♂ were caught by the *Cataglyphis*. I caught a

winged ♀. In great excitement, the large *Messor* ☿ drew a ♂ from time to time back into their nest. The biggest ☿ took no part in the battles with the *Cataglyphis;* they seemed to be acting merely as a police-force inside the nest.

May 20th—23rd. A very hot day. The main openings of the *Messor* nests were closed, and a few small ☿ only were labouring near the refuse-hole, throwing out a little earth and seed-debris.

June 1st. After a slight shower, the *Messor* set out on their old road in search of seeds for the first time that year. I saw several large ☿ on patrol, coming and going along the borders of the path, but not working. Throughout the days that followed, absolute peace reigned once more, but the *Cataglyphis* ♂ began to come out again, though they did not fly away. In this connection, Santschi wrote to tell me that he had received an ergatomorphous ♂ of *Cataglyphis albicans*, together with the ordinary winged ♂: hence we have here, as in *Ponera Eduardi*, a winged ♂ and an apterous ♂ in the same species."

The above observations, made by such a conscientious observer as Brauns, are very instructive. We shall see their complement in Part V, in his observations entirely devoted to *Messor*. Between the two above-mentioned species, a very small, greyish ant, probably a *Cardiocondyla*, would run out of the cracks in the ground, but took no part in the fighting.

My friend Dr. Santschi wrote to me from Tunis on the subject of wars between ants, and confirmed the impression that I had gained during each of my three visits to that country and to Algeria; the ants of those parts are much less bellicose towards each other than those of Europe; one scarcely ever sees them fighting. Can this be because the struggle for existence is less intense? He once saw some *Monomorium Salomonis* quarrelling with some *Tapinoma*

nigerrimum which had approached them, but this was a minor affair. We have an exception to this, however, in the *Dorylinæ*, particularly *Dorylus* with its underground hunting expeditions, as I have often observed by reason of the corpses of these ants which I found, intermingled with those of *Cremastogaster* and others, while turning up the sand or earth with my chisel. Santschi wrote to tell me that he has several times observed the hurried exodus of the *Messor* from their nest, with all their brood. On each occasion, when he dug into the nest, he found the galleries invaded by *Dorylus fulvus*, which had attacked them.

W. M. Mann, who has studied the ants of Australia and tropical America, wrote to me: "Apart from those of *Eciton*, I have seen no warfaring excursions by ants comparable to those of the European *R. sanguinea* and *Polyergus*. Many species, such as the American *Neoponera* and *Pachycondyla*, seem to me extremely cowardly. The Australian *Myrmecia*, however, is an exception. In the midst of a picnic on a flat rock in Australia, we were forced to run away from the *M. gulosa*, which had a mania for suddenly stinging our legs."

Dr. Carlos Bruch of La Plata (Argentine) wrote to tell me that he had seen few ant-wars in that country, except for those of *Eciton*. He is inclined to support the idea that in many cases, at any rate, a kind of pacific parabiosis between ants under the same stone is more common than a state of warfare. For instance, he found colonies of *Pheidole taurus*, *Pheidole obtusopilosa* and *Solenopsis Richteri* (a variety which does not live in lestobiosis) dwelling together in this fashion. After lifting the stone he observed these species and their brood for a considerable time. They would pass by without doing each other the slightest harm; so likewise did some *Rogeria Foreli*, *Sol. Richteri*, *Brachymyrmex* and *Ponera trigona*.

Nevertheless, Bruch has observed wars, both natural and artificially incited, between various colonies of *Sol. Richteri;* they fought furiously, and even beheaded several enemies, which a number of them would attack in the neck at the same time.

In his experiments with myrmecophilous beetles, Bruch also intermingled *Sol. Richteri*, *Acromyrmex*, *Trachymyrmex* and *Apterostigma* of various colonies, without inducing them to do each other any harm.

If we compare the observations of all these authors and those which I myself have made, we come to the conclusion that, apart from the *Dorylinæ*, our ants of Europe are the greatest fighters and aggressors—just like the humans, alas!

The most terrible of our European ants is indisputably *Neomyrma rubida*. But, instinctively conscious, no doubt, of the power of her sting, she is usually very peaceful, much more so than *M. lævinodis*. I have never seen her make a spontaneous attack upon other colonies. However, when I poured out a bagful of *F. pratensis* on to a *N. rubida* nest, I saw the ☿ surround the heap of *Formica* and kill them all with their stings in less than an hour—not a single *rubida* being killed. In the same way, they kill *Polyergus* in a moment. A few *N. rubida* which were placed on a large polycalic colony of *Formica cinerea* survived among their myriads of enemies for two hours, during which time they killed many more than their own numbers. Similarly, some more *N. rubida*, when put on a large nest of *F. rufa*, resisted these opponents for a long time and killed many of them; some of them even managed to escape through the crowd of *rufa*.

In September, 1867, I placed a large heap of *T. cæspitum* of a large-sized variety a decimetre away from one of the nests of a colony of *Pheidole pallidula*. The alarm spread like wildfire, and hundreds of *Pheidole* ☿ hurled themselves in

front of the foe. But all the same the *Tetramorium*, being infinitely stronger and more robust, obtained the upper hand of them and advanced resolutely towards the nest, killing a host of *Pheidole* ☿, which still remained attached to their legs after succumbing to a single bite or thrust of the sting. A considerable number of soldiers then gradually came on the scene. They advanced with open jaws, dealing out threats to left and right, and thus succeeded in frightening several *Tetramorium* ☿ and causing them to withdraw. These soldiers tried specially hard to avoid being grasped by the legs, and to seize their adversaries in the back. If they achieved this aim they at once squeezed the neck of the *Tetramorium* with all their might, and promptly cut through it. But if a soldier was compelled to fight hand to hand with a *Tetramorium*, the match was uncertain and the victory often went to the latter, especially if she took hold of the soldier by one of its mandibles. If a *Tetramorium* tried to get into the nest, a soldier posted at the door would bite at her violently and make her lose her balance, enabling the ☿ to drag her into the subterranean passages. The ☿ always retired gradually from the fray, whereas the number of soldiers increased, and finally the *Tetramorium* were routed by the force of numbers and withdrew the poorer for many of their companions which had been decapitated.

CREMASTOGASTER SCUTELLARIS, like all the *Cremastogaster* species, fights by curling her abdomen upwards, not downwards (see fig. 100 *A*), thus drenching her adversary with poison, rather than by pricking with her weak sting. *C. scutellaris* fights with fury and concerted effort: the ☿ sprinkle poison on the heads of the ♃, which attempt, usually in vain, to cut off one of their limbs.

POLYERGUS RUFESCENS AGAINST RAPTIFORMICA SANGUINEA. It is interesting to bring about a conflict between these two

slave-making species, one of which is more enterprising and impudent than the other in its thefts. *R. sanguinea*, though larger and more wily in her tactics, is, however, less daring, less strong in endurance and less rapid in individual or concerted action than *P. rufescens*, whose curved and pointed mandibles she lacks. In 1869 I put a formicary of *Polyergus* in an apparatus barely 2 metres from a large colony of big *R. sanguinea* situated at the edge of a lane. Several *fusca* slaves came out of the apparatus and were killed by the *sanguinea*, which rushed to the lane in large numbers and came near the communication-tube of my apparatus. About ten *Polygergus* ♀ then ran out and flung themselves at the head of the *sanguinea* army. But in vain did they snap with their jaws to left and right like mad things: the enemy front, like an ever-widening sea of red, swallowed them up, and they were soaked with poison. At this moment I saw about sixty *Polyergus* come out of the indiarubber tube of the apparatus and fall upon the *sanguinea* front, darting into their midst, biting to left and right and finding some means of extricating themselves even when ten or twenty of the enemy were engaged with each of them. The entire mass of *sanguinea* then retreated to the edge of the lane and the doors of their nest, whither they were followed by the sixty *Polyergus*, more valiant than the 300 Spartans of Leonidas. After each single combat the *P. rufescens* would stop to brush their abdomens and back legs. Soon the *sanguinea* lost all courage and their slaves began to bring the nymphs out of the nest. In less than five minutes a wild panic seized the famous *Raptiformica*, which rushed out in a crowd, carrying their nymphs and escaping into the grass. They even abandoned most of their young, like cowards, and left them in a white mass all over the dome. In ten minutes' time the nest was emptied. Half of the

Polyergus had been killed, but the thirty remaining victors bore a few nymphs into the apparatus. Two minutes after, the whole *Polyergus* army, which had not yet moved, came out through the tube, went to the conquered nest, carried off the nymphs and filled the apparatus with them. All this continued until half-past eight. The *sanguinea*, which had made themselves a provisional nest in the grass, dared not return to their empty nest until several days later.

The following observation was made afterwards on June 26th, 1907, at Chigny near Morges, where I was then living. On the top of a wall 2 metres high, which was on a level with our terrace, stood a large formicary of *F. sanguinea*. This wall edged a road, which was therefore 2 metres lower than the terrace. On this occasion, at about 1-30 p.m., I saw the *sanguinea* run down the wall towards the east, and cross the road obliquely in groups.

Supposing that they were going on an ordinary expedition, I looked for a colony of *glebaria* on the other side of the road, but instead of this I discovered one belonging to *Polyergus rufescens*, whither the *sanguinea* were directing their steps.

As I was in a hurry, I hastened matters by placing a few *glebaria*, with their cocoons, together with two *Polyergus*, before the *sanguinea* front. The two *Polyergus* flung themselves upon the enemy in their customary manner, like a pair of Japanese practising ju-jitsu. But they were killed. I then went and fetched some more *glebaria* from another (ordinary) formicary to hasten the encounter, which was not long in occurring, as the *sanguinea* had already crossed the road and were carrying off the *glebaria* cocoons. At this moment the *Polyergus* of the nest began to run out.

Then began one of the most comical scenes I have ever witnessed in my life. The *sanguinea* had doubtless imagined that they were going to attack an ordinary *glebaria* nest, and

my bait had whipped up their courage still further. But they had reckoned without their hosts! Between twenty-five and thirty *Polyergus* came out of the nest and began their usual ju-jitsu against this impudent foe, which fought with much energy. A single *Polyergus*, however, thanks to her tactics, overcame five or seven adversaries almost simultaneously. What is more, the terrible hooks of the *Polyergus* clove through the brains of several *sanguinea*. Then only did the aggressors begin to understand their mistake and to withdraw, slowly at first, while the numbers of the *Polyergus* increased visibly. The real battle began at half-past two; at a quarter to three, the *sanguinea* were completely routed and rushed up the wall again to their nest, followed as far as the middle of the road by the *Polyergus*. During the days that followed, they took good care not to come back.

The interesting fact about all this is that the strife between the two bands of brigands had been spontaneous, whereas in the preceding case I myself had instigated it. Although the *sanguinea* colony was very large, as was also the size of its ☿, it would have been obliged to flee in utter confusion if the *Polyergus* had been minded to go farther and climb the wall. Moreover, the fact that the *sanguinea* took care not to re-open hostilities proves that individual memory had been acquired by their defeat. According to the theory of tropisms propounded by Loeb and Bethe, they should have begun all over again.

LARGE AND SMALL SPECIES. Plate XV, which depicts from nature a fight between *Formica pratensis* and *Tetramorium cæspitum*, explains the matter better than any written description. As soon as they have the numerical advantage, the small ones grasp hold of the large by their limbs, and try to sting them or cover them with poison. The large ants, for their part, strive to crush the small ones between their

mandibles. The very small ones, such as *Solenopsis fugax*, often escape the notice and even the antennæ of the large. Moreover, the openings of their nest, especially when their ♀ are not too big, are not wide enough to admit of raids by the others. In this respect our *Lasius* are ill-protected.

DORYLINÆ. We have already described how the *Dorylinæ* make war, not only on insects in general but also on other ants, in order to steal and devour their brood, and often to steal their nests provisionally also. Sjöstedt had observed how the *Cremastogaster* of tropical Africa, which nest in the spines of certain acacias (Plate VII *b*), contrive to defend themselves against the attacks of the *Anomma:* they place the tips of their abdomens all together near the single hole in the spine which serves them as a door, and so block it up. As soon as an *Anomma* puts its head near the hole, they besprinkle it with their caustic poison and so manage to defend themselves and drive off these terrible enemies. I have already fulfilled my duty to my readers by telling them how an *Azteca* puts an *Eciton* to flight by sprinkling her with poison from her anal gland.

5 COLD-BLOODED FIGHTING. I used this term in 1874 to denote combats, mostly of an individual character, wherein certain ants, using neither poison nor sting, persist in torturing to death others which offer no defence and play a purely stoical and passive rôle. In Chapter I, §§ 2 and 5, I have described some typical cold-blooded fighting between *Leptothorax* of the same species, and also betweeen *Formica sanguinea* and *pratensis*. Fig. 96 is a faithful representation of such a combat, in which *F. sanguinea* is the active Inquisitor. This behaviour is most commonly manifested after an alliance, by a few particularly vindictive individuals which cannot be reconciled to the newcomers adopted by their companions. It may be that the difference in odours

alone suffices to account for these facts, as Miss Fielde suggests, or other sentimental causes may have a share in explaining them.

The executioner puts her victim to death by methodically sawing off her legs and antennæ, one after the other. Sometimes she also saws through the neck, but more often, when she has finished mutilating the creature, she contents herself with carrying her some distance from the nest and throwing her down. Having lost her antennæ, this ant is incapable of finding her bearings and of returning to the nest. We have dealt with the milder method of cold-blooded fighting adopted by *Leptothorax*, which carries the ant she hates as far away as possible and then throws her down without mutilating her. At various times I have observed some hundreds of cases of this sort.

All these observations of collective spite between ants are, alas! so poignantly reminiscent of our wretched human society that they cannot but wring the heart of every man with moral—that is, social instincts. This is the obverse side to the social world of ants.

Chapter IV

WARS BETWEEN ANTS, OTHER LIVE CREATURES, AND NATURE

The offensive and defensive wars of our little friends, dear reader, are waged not only against other ants, but also against other living creatures and inanimate nature. We will begin with lifeless things.

We have seen how ants brave the desert with their psammophores, and drought with their nurses and deep-laid granaries. With their domes and with stones they protect themselves against heat and frost and regulate the temperature for their brood. Here they make use of the earth and sun. But while they must have water on the one hand for their subsistence and building operations, they must needs find some means of preserving themselves on the other hand against its ravages, which are sometimes alarmingly sudden.

In Part III, Chapter VI, we have described ant-gardens, a lasting and fundamental provision against the more or less perpetual floods of certain tropical countries. Against sudden temporary floods they have another ingenious defence. Long ago Savage described how the *Anomma* in Africa manage to save themselves and their brood from such dilemmas. They mass together to form a living ball of ants, in the centre of which the brood is placed. This ball contains air, which enables it to float. In dry weather, *Eciton* sometimes makes provisional nests of a similar character in bushes, which

need not astonish us. A more surprising fact is related by Ihering with regard to *Solenopsis geminata*. This ant, which builds its nest in the earth, behaves in an almost identical fashion during the temporary floods of Brazil. Ihering caught sight of some clumps 16 to 25 centimetres long, consisting entirely of the ☿ of these *Solenopsis*, firmly interlocked with one another and floating on the water of the flood; and inside these clumps, well protected and perfectly dry, were the brood and all the members of the winged sexes. He says that *Atta* will behave in a similar way.

We shall understand this matter still better if we compare it with the fact that ants can endure lengthy submersion without perishing. I have often observed this myself, and Miss Fielde's experiments are absolutely conclusive in this matter. She saw some ants completely revive and recover after three to seven days of total submersion; four *Camponotus pennsylvanicus* out of seven recovered after being under water for eight whole days. This was the longest survival. Miss Fielde invariably found that the large ☿ were capable of greater endurance, against both submersion and fasting, than the small ones.

When the *Anomma* are out on their hunting-expeditions in tropical Africa, a stream cannot stop them. They cross it by a living bridge of ants, which they form by linking themselves together on some object projecting from one bank until the chain thus made finds some other support—a stone, twig, grass-blade or some such thing, on the other bank. The ☿ then link themselves with this object, the chain spreads out and the whole of the greedy robber-army continues its depredations on the other bank, passing over the living bridge formed by their own companions. Thus it comes about that ants can brave the water, thanks to their collective social organization.

In Part II, Chapter IV, we have already mentioned the synechthrans, their guests or neighbours, which confront ants and attack them on the very threshold of their nest, with or without mimicry. These are terrible enemies, in the form of beetles, bugs, spiders, etc. When a spider enmeshes them in its web, ants sometimes manage to defend themselves by catching hold of one of its legs between their mandibles. The spider then lets go, and if the ant holds fast she may succeed in detaching the leg of her enemy, which cuts it off itself. Sometimes the ant herself then manages to escape from the threads. After an affair of this kind, I have known the spider philosophically turn its attention to devouring its own leg which has remained entangled in the threads, and which it has itself amputated in its fright. Thus nature ordains that nothing shall be wasted.

Among the ants' most terrible enemies, we must mention the larvæ of lace-wings, known as ant-lions, which in our own countries lie in wait for other ants in little funnels of sand, throw out sand from the bottom to cover them, and then catch and eat them. Then there are certain mammals, such as the ant-eater of America and the pangolin of Africa, with their scaly hides, the hedgehogs and others, which take hold of ants, even the *Dorylinæ*, with their long, sticky tongues and swallow enormous numbers of them. I have extracted plenty of interesting species of ants—even some which were new, that is, hitherto unknown—from the stomach of a single pangolin. I even named one of them '*esta*,' which means 'eaten.'

The *Machæromyrma* of the Sahara have a 2|, which will be depicted in Plate XIV, *i*, and which I think must be intended to bite the tongues of the hedgehogs, as it bit me when I demolished its nest. Certain birds, the green woodpecker and many others, ravage the formicaries of ants

such as *F. rufa*. I have seen bird-excrement consisting exclusively of the corpses of *Myrmica*.

I presume, moreover, that the curious spines of certain *Polyrhachis*, which may be straight (Plate XIII, *b*,*c*,*d*) or curved (Plate XV), are developed for the sole purpose of injuring the stomach of birds or mammals which swallow the ant, and thus giving it a distaste for such prey. These ants live in small colonies in woven nests, either on or under leaves or sometimes between them, but rarely on the ground, and birds are their worst enemies. I do not see how their spines could be used as weapons against other ants.

With regard to the offensive wars waged by ants against other animals and against plants, we have already given an account of the numerous insects which *F. pratensis* kills and carries over her roads. In Part V we shall describe the plunder-raids made by the *Dorylinæ* against animals, and the thefts of tree-foliage perpetrated by the *Attini*. Furthermore, nearly all the *Ponerinæ* live exclusively on the insects they kill, and many *Myrmicinæ* are scarcely more peaceful. It is chiefly the *Formicinæ* and *Dolichoderinæ* which live on their cattle and the nectar of plants, though they do not all do so, as we have already seen in the case of *Formica*.

It still remains, dear reader, to speak of the wars waged by ants against their social peers the termites, wrongly called 'white ants,' whose habits are almost as interesting as those of our little friends. In this case, we must confess, the ants are always the aggressors and the termites the victims.

Several whole genera of ants feed almost exclusively on termites; these are nearly all genera of the *Ponerinæ*, such as *Leptogenys* (including s.g. *Lobopelta*), *Diacamma*, *Ophthalmopone*, and others in all tropical countries. These attack the termites relentlessly; though other ants, such as the *Formicinæ*, *Dorylinæ* and *Myrmicinæ* do not despise them either,

as M. Bugnion has shown. At Biskra I myself have seen *Cataglyphis Diehli* bearing termites between its mandibles. Alfred Ilg, a former minister of King Menelik of Abyssinia, wrote to me as follows in 1894, when he sent me a specimen of *Ophthalmopone Ilgi*, his discovery, which I dedicated to him.

"One of my servants told me that if I wished to see a large number of ants I had only to come an hour before sunset, as a whole army would then come out of a hole and afterwards disappear. Wishing to investigate this mystery, I posted a man in front of the hole before the ants appeared, and hurried thither as soon as he announced that they were beginning to come out. I then saw a number of great black ants emerging in close ranks, and assembling in front of the hole in considerable force.

Suddenly the whole band set out in a close file as though guided by a chief, while a company of fifty or less stopped for a moment in front of the hole and soon went into it again. I then cautiously followed the marching file to a distance of some 50 metres, consumed with curiosity to see where it was going. As it turned towards my luggage, I began to suspect that the ants wanted to steal my rice. But to my surprise they crept under my water-bag, and I thought then that they were thirsty. Not at all: on raising my water-bag cautiously I found those villains of ants engaged in a furious fight with some termites which had been attracted thither by the moisture, as they usually are in the desert. Despite the gallant defence put up by the termites, each of these black rascals seized one of the poor little creatures between her shining mandibles, cut through it, lifted it up in the air and returned home with her prey as quickly as the grass and stones permitted. I was surprised to see a fairly large ant, which had come up to a distance of about

2 metres from the battlefield, halt every companion which carried a termite as soon as she arrived, until they were all collected in one place, laden with the hapless victims. But that was not all: between thirty and forty ants relinquished their prey and returned to the battlefield, not to pick up termites this time, but to take charge of some of their companions which were still prowling about there, and which seemed to me to be wounded. They took them by the mandibles and bore them off to the general assembly, which was waiting. As soon as there were no stragglers left, the whole troop returned home laden with prey and the companions I supposed were wounded, and disappeared again into the hole."

The hole in question evidently contained the nest of the *Ophthalmopone*, and the ants which Ilg thought were wounded were probably ☿ which had strayed and could no longer find their path. It is possible that they had been sprinkled by the termites with some juice. This observation is very interesting because of the light it throws on the order observed by the *Ponerinæ* in their 'termitophagous' expeditions.

Megaloponera fœtens carries out similar expeditions which are no less interesting. When this ant goes hunting termites, it stridulates so loudly that human ears can perceive the chirping, according to Prell, at a distance of 1 or 2 metres. Ilg sent me a specimen of this species from Schoa in Abyssinia, and confirmed Prell's statement that its stridulation is audible and that these ants go out termite-hunting in troops.

My friend Wroughton wrote to me as follows about the expeditions of *Lobopelta processionalis:* "This ant is common in the neighbourhood of Poona in India, and has well-disciplined armies like all the other *Lobopelta*. The ☿ which are encountered singly are probably only scouts. They are

usually seen very early in the morning or else quite late in the afternoon, journeying in unbroken columns six or eight wide, and following a straight line, or rather the easiest route, to the field of action, which usually consists of a termite-nest whose galleries have been broken by the hoof of a horse or ox, or in some other way. Once the army reaches its destination, each ☿ seizes a termite, places it under her thorax in the manner typical of the *Ponerinæ*, and the whole column returns with its burden to the nest; but the return journey is much more easy-going and less regular than the out-going one."

Bingham has confirmed Wroughton's statements in connection with *Lobopelta chinensis*, *birmana* and *Kitteli*, which march four-deep, whereas *L. Binghami* and *aspera* march only in single or double file, or even go hunting separately, as *Diacamma* does. Dahl has made observations on some *Lobopelta bismarckensis* which were marching in a troop of about fifty to attack termites.

In the last century, Bates saw the enormous *Dinoponera grandis* marching in a file across the undergrowth of the virgin forest of Brazil (probably also termite-hunting). As Wheeler says, all this recalls the expeditions of the *Dorylinæ*, and also those slave-making raids which we shall discuss shortly.

Here I may pause to refer my readers to the Appendix at the end of this volume, written by Professor E. Bugnion, who spent several years in Ceylon observing the defensive wars of termites against ants. The observations in the excellent book on Africa which M. Hegh has recently published are also summarized in this Appendix.

Chapter V

PARABIOSIS OF CERTAIN ANTS

One day in 1896, whilst I was walking along a forest path in the neighbourhood of Santa Marta in Colombia, I was interested to see a file of black, shiny ants belonging to two very different species, which seemed to be living together on the best of terms. One of them was very

Fig. 99

small, the other notably large. They were crossing the path, some on the way back to the nest, their abdomens swollen by their crops, others marching in the opposite direction on a plundering raid. I examined them under the magnifying glass; the large species proved to be *Dolichoderus* (*Monacis*)

debilis, of a variety which I afterwards named *parabiotica*, and the small, *Cremastogaster limata*, of a new and tiny race which I baptized with the same name, *parabiotica*. Hence they belonged to two different sub-families, the *Dolichoderinæ* and *Myrmicinæ*. Fig. 99 represents, on a scale almost five times the natural size, an oblique view of the file in question, with (1) four *Cremastogaster*, two of which have their abdomens curled upward, and two *Monacis*, going marauding; (2) nine *Cremastogaster* and nine *Monacis* returning home with full crops. All are drawn from my specimens gathered in Colombia.

I was much intrigued, and first followed those which were going marauding. I saw them climb on to the bushes and finally separate into species, the *Cremastogaster* going off to milk aphids and the *Monacis* to suck the nectaries of flowers. But they afterwards rejoined each other and returned in a common file like friends to their dwelling, keeping close to one another as shown in our figure.

I then turned to the other side of the path and followed the common file which was climbing up and down the trunk of a tree. Fortunately for me I was not obliged to climb it myself. I had only mounted halfway when I saw all my ants enter a large termite nest which they had stolen, as they are wont to do, from its makers; but they had only part of it, for about a third was still occupied by termites. On destroying a corner of the nest by which the ants were entering, I saw within it a social idyll such as I have never seen since. The chambers which had formerly belonged to the termites were occupied both by *Monacis* and *Cremastogaster*, each with its brood and some of its winged sexual forms. *But they were not living in a haphazard colony! Although the chambers occupied by each species were partially fused with the walls of those occupied by the other, all the apartments were*

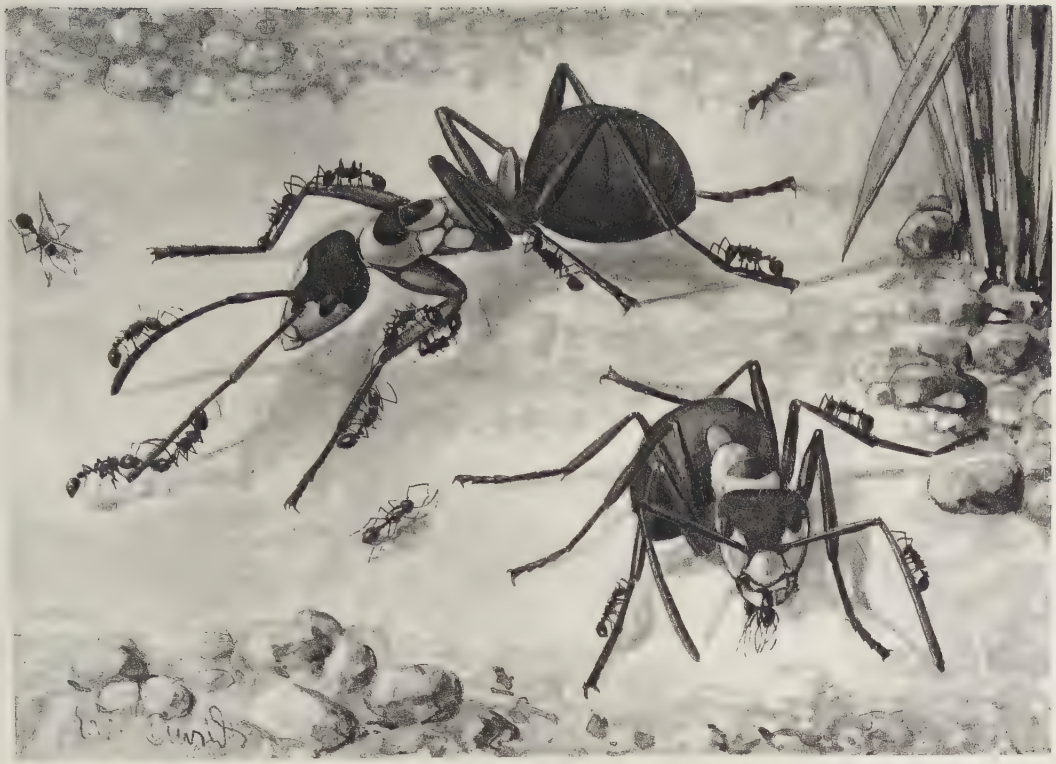
Battle between ants of different species (*Formica pratensis* and *Tetramorium cæspitum*).

IX. 19

Nov. 11.

Battle between an old English species (Lowland variety) and a new one of Irish origin.

(Illustrated London News, 1st June 1861, p. 561.)



clearly separated from one another, somewhat like those of lodgers in the same house. Each species had its brood and its winged forms in suitable chambers. Nevertheless, my breach did not occasion the slightest disturbance. Each individual concerned immediately moved by common understanding into other chambers.

I stood thunderstruck at the thought of such a thing, which was then absolutely new in the annals of myrmecology. After due reflection I baptized it with the name of *parabiosis* (life side by side). One point here deserves note: in Colombia I found other files of a similar character formed by the same two species but I never discovered their common nest. I also found *Monacis debilis* v. *parabiotica*, however, in isolated nests, without *Cremastogaster*, and similarly *Cremastogaster limata parabiotica* without *Monacis*. Parabiosis between the two species is therefore facultative and free, and involves neither a mixed colony nor a composite nest inhabited by enemies.

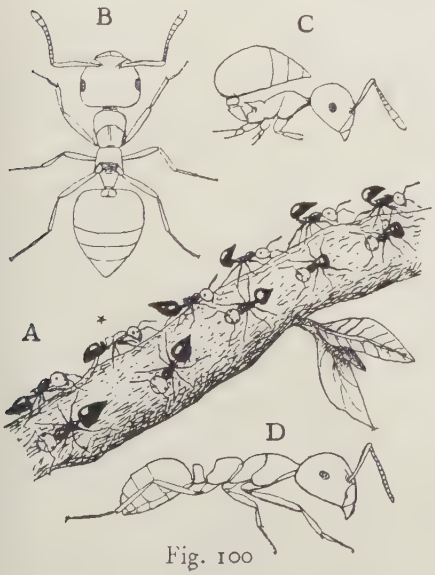


Fig. 100

You may imagine, dear reader, how this discovery opened my eyes to other cases, more or less analogous, to which I had not hitherto given enough thought. In Tunis and Algeria in 1889 and 1893, I had already observed some *Camponotus* (*Orthonotomyrmex*) *lateralis*, with red heads and black bodies (fig. 100 *A* and

D) running about separately on the cork-oaks, among some *Cremastogaster scutellaris* of the same size and colour (fig. 100 *A*, *B* and *C*), neither species doing the other the least harm. Emery, whose figure I have borrowed, has made similar observations in Italy. Here, however, the nests are entirely separate and the friendship is not intimate. It seems more as though *Camponotus*, under cover of mimicry, were merely creeping in among the much more numerous and better-armed *Cremastogaster*, in order to seek prey under their protection, on the analogy of the synoeketic guests of ants: they are tolerated, but not liked, and the parabiosis is incomplete. The same thing probably obtains with the two cases of mimicry depicted in Plate IV, *e* and *f*, and also *g* and *h*, in Part II. In one of these, *Camponotus imitator* (*h*) is creeping in among *Aphænogaster Swammerdami* (*g*), of Madagascar, to gain access to plants where it can seek resin-coccids; in the other, *Dorymyrmex ensifer* is running along the sand in the Argentine among some *Conomyrma exsanguis*, with which it seems to be constantly found—why, we do not yet know.

In Switzerland, the three typical infesters of the walnut-tree, especially *Colobopsis truncata* and *Hypoclinea quadripunctata*, are perpetually jostling together about the twigs without attacking or injuring each other in any way. But when enclosed together in a flask, they separate and post themselves at the doors of their respective dwellings, showing their teeth occasionally but still never fighting. This is a tendency towards parabiosis.

Wheeler discovered a kind of parabiosis in Mexico and Florida on an epiphytic plant of the genus *Tillandsia*. This plant looks like a bud 5-8 centimetres long by 4 in diameter, the leaves being compressed one against the other. Inside it, ants of the genera *Pseudomyrma*,

Monomorium, *Xenomyrmex*, *Cremastogaster*, *Leptothorax*, *Cryptocerus* (*Myrmicinæ*), *Tapinoma* (*Dolichoderinæ*) and *Camponotus* (*Formicinæ*) very often hollow out, in or between these tightly compressed leaves, little nests into which they pack themselves and their brood like so many sardines. The formicaries of various comparatively timid and peaceful species of the above genera are fairly often found together on one *Tillandsia* in such a manner that the nest of each occupies the whole or part of the space enclosed between two leaves, although it is often completely surrounded by the nest of another species, and sometimes situated in the heart of the plant. It is easy to realize that war between formicaries of this kind, whose apartments are so close to one another, must be dispensed with; Wheeler declares that the mutual relations between these ants may be either friendly or neutral. Here, then, despite the multiplicity of genera, we have another case of parabiosis. As in my Colombian instance, it is not necessary to any of these species, but is a mere accident.

According to Escherich, *Cremastogaster victima* r. *alegrensis* always lives in the nest of a species of termite, *Eutermes fulviceps* of Brazil, and, apparently, in perfect harmony with it. Hence this may, as he supposes, be a form of parabiosis, this time between ants and termites. Similarly, *Camponotus punctulatus* r. *termitarius* lives in the Argentine in friendly parabiosis with termites (*Eutermes*, *Anaplotermes*). But this is a sort of syndiacony, fairly constant in character; the termite provides the ant with a dwelling-place while the ant defends the termite from the ravages of various other ants. Wasmann has applied to this variety of parabiosis the special name of *phylacobiosis*.

Parabiosis may, therefore, be defined as follows: the natural and free social relations between two or more

communities of ants, or between ants and termites, each keeping its apartments and brood separate from the other. These relations may vary between friendship and neutrality. Parabiosis, therefore, constitutes a transition between war on the one hand and the intimate alliances of mixed formicaries on the other. The habits of certain parasitic ants, such as *Leptothorax Emersoni*, constitute another form of transition between parabiosis and the mixed formicary.

You see plainly enough, dear reader, there are gradual transitions everywhere in this world.

Wheeler has given an account (*Ecology*, Vol. II, No. 2, April, 1921) of various new cases of parabiosis. In the first place, he himself found at Panama and Guatemala eight mixed colonies belonging to the same *Monacis debilis* v. *parabiotica* and the same *Cremastogaster parabiotica*. They were living together in separate chambers of one nest, either a termitary or a construction built in decayed wood. They went out together as friends in common files. The whole story confirmed my observations in every respect. Wheeler once saw the two species sharing some Membracidæ, which they were milking on a bush. He also found some isolated *Monacis* colonies. Christophersen also confirmed my observations in Panama.

In 1913, moreover, Wheeler discovered in Central America a case of polycalic parabiosis between *Camponotus* (*Myrmobrachis*) *planatus* and *Pseudomyrma Belti* v. *fulvescens*, which lived in different spines of the same acacia-branch, but went out together in search of plunder.

While in Brazil in 1912 Mann discovered two new cases of parabiosis, one between the powerful *Monacis bispinosus* and *Cremastogaster parabiotica*, the other between *Monacis debilis* v. *rufescens* and the big, strong species, *Odontomachus affinis* r. *Mayi*, which stung him severely.

The two species lived together in one ant-garden situated 40 feet above the ground, on a tree which was to be cut down. Wheeler likewise observed in Guiana some *Camponotus* (*Myrmothrix*) *femoratus* living in parabiosis with *Cremastogaster parabiotica* in communal ant-gardens.

In short, the number of well-authenticated cases of parabiosis is increasing every year, and now forms a complete scale of transitions between warfare and the mixed formicary.

Chapter VI

LESTOBIOSIS AND CLEPTOBIOSIS IN ANTS

1 Lestobiosis

In 1858, when I was ten years old and was staying with my grand-parents at 'La Gracieuse' near Morges, I observed some very small yellowish-coloured ants making their homes between the walls of nests belonging to *Formica fusca* v. *glebaria* and *rufibarbis*, and sometimes those belonging to other species also, but always keeping to the side of the nest. I saw these little ants passing along their minute passages, which were inaccessible to *F. glebaria*, and devouring the brood of the larger species, whose adult ants they fought like little fiends as soon as I destroyed the nest. My grandmother, as I said in the Preface, had given me Pierre Huber's book the previous year, and when I found to my surprise that it contained no information as to the habits of this diminutive ant of mine, I observed it all the more attentively. At a later date I learned its name from Mayr. It was *Solenopsis fugax*, and its nest represented the type which I described as 'double' in 1874. At the age of twenty, I became a member of the Swiss Entomological Society, and finding that the habits of my little ant had never been described, I ventured in 1869 to publish my observations on the subject in the Bulletin of the Society. This was my first publication.

These murderous habits were afterwards observed in several other genera of small ants, as well as in many species

of *Solenopsis*, and I applied to it the name of lestobiosis, which means 'life as a brigand.' In actual fact, lestobiosis is nothing more nor less than collective synechthry, analogous to the individual synechthry of *Myrmedonia*, etc., which we have discussed in Chapter IV of our Part II. But as in this instance the synechthrans are ants, and therefore social creatures, they can scarcely find a better way of thieving the brood of other species than by building their own nests side by side with them.

Fig. 101

In order to understand lestobiosis, therefore, we must understand the character of the nests built by the little murderers. Fig. 101, after Wasmann, represents in white the large passages belonging to the nest of the large ant and the small passages of the little murderer, which open into them, the solid material between being left black. But all this is too

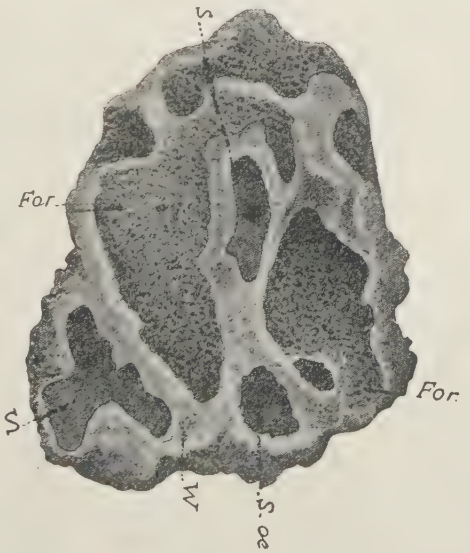


Fig. 102

theoretical and schematic—though sometimes it is to be actually seen under a stone. We have a more realistic example in fig. 102, drawn from a natural nest hardened with silicate. Here the chambers of *S. fugax*, *S.*, recognizable by the very fine grains of earth used in their construction, were encased in the walls between the large chambers of *F. glebaria* with their much coarser grains. At the bottom some of the little holes of the *Solenopsis* are visible. But the *Solenopsis* chambers themselves are not particularly small, since they have to afford room for the fertile ♀ and the big larvæ and nymphs of the winged sexes.

S. fugax makes fearful onslaughts upon the brood of *Formica*, most of which it devours, usually without being perceived, since the *Solenopsis* ☿ can escape their eyes and almost escape the touch of their antennæ. Moreover, as it runs lightly over the brood, *S. fugax* often catches it alone and unguarded. When one of these large double nests is destroyed it is extraordinarily amusing to watch the big *Formica*, covered with small yellow *Solenopsis* which are stinging them, bite the earth around them in their fury and, as a rule, miss their little enemies. If they chance to catch one between their mandibles, they crush her without difficulty: but this is more easily said than done. Meantime, the *Formica* often succumb to the numerous stings inflicted upon them by their wicked little foes.

The *Formica* of the *fusca* group are not the only species in whose walls *S. fugax* will secrete her nest for the sake of carrying on her lestobiosis, but she will sometimes infest *F. rufa* and her kindred *Polyergus*, *Lasius*, *Tetramorium caespitum*, *Pheidole pallidula* and even *Myrmica*. Nevertheless I was compelled to recognize, even in my young days, that *S. fugax* is not absolutely dependent upon this means of livelihood, but that she sometimes dwells in isolated

formicaries with simple nests, expecially in stony places, and that she is very well acquainted with the art of licking and cutting up dead ants and even that of rearing aphids. Certain other species of *Solenopsis* do not live in lestobiosis at all; these are mostly the larger species, such as *S. geminata*, *sævissima*, *globularia*, etc.

The observations of my childhood have since been confirmed by a large number of others concerning many ant-genera, in several of which lestobiosis seems to be constant, and therefore much more exclusive than it is in *S. fugax*; this is true of several *Solenopsis* species which are extremely minute, much more so than *S. fugax*. The genera *Carebara*, *Carebarella*, *Pædalgus*, *Oligomyrmex*, *Aeromyrma*, *Diplomorium*, *Tranopelta* and *Erebomyrma*, which live almost exclusively in lestobiosis, may also be cited. To these Wheeler adds certain species of *Monomorium*, *Cremastogaster*, *Pheidole* and even *Tapinoma* and *Brachymyrmex*. But lestobiosis is also extended to the termites, inasmuch as they passively endure hardships at the hands of the ants. A fair number of the little murderers, such as *Carebara*, *Pædalgus*, etc., attack termites only.

♀

Fig. 103

We may state as a general fact that all ants which live in lestobiosis have small ☿, perhaps exceptionally small ones, the most diminutive being sometimes only ·8 or ·9 millimetres long, whereas the winged sexes, especially the ♀, are often very large, even enormous. I must request my readers to look at fig. 103, which represents the

minute worker of the African *Carebara vidua*, at two and a half times her natural size, and side by side with her, the enormous ♀ of the same species. This is an extreme case, and seems almost incredible, though it has been adequately demonstrated. I even possess in my collection ♀, ♂ and ☿ of two races of this species, taken in termitaries. Such fantastic polymorphism can probably be explained by the gradual disappearance of the ♃ or large ☿.

Having settled this matter, let us turn to special examples of ants, other than *S. fugax*, whose habits are similar to those described above.

I have myself found in Algeria two *Solenopsis* much smaller than *S. fugax*, living in apparently constant lestobiosis; one of these is *S. latro*, found in the nests of *Aphænogaster sardoa*, the other *S. oraniensis*, found in those of *Leptothorax Rottenbergi*.

S. orbula was described by Emery and taken in similar circumstances. Many other tiny *Solenopsis* found in America and elsewhere are similar. Their colour is a very pale yellow, evidently due to the fact that they spend most of their time underground, and their eyes are reduced to two small black dots. On the anterior edge of the epistoma, however, they have small, sharp teeth which they probably fix in the skin of the brood of ants and termites, while trying to hack them in pieces with their mandibles.

Wheeler thinks that his *Pheidole lamia*, which has a ♃ with a head truncated in front, and several species of *Strumigenys* live in lestobiosis in the nests of other ants. *Pheidole calens* lives in double nests together with *Pogonomyrmex barbatus* of Mexico. Wheeler thinks that its chief aim is rather to steal a few of the seeds gathered in by the large harvesting ant than to murder its brood.

On the other hand, Dr. Hans Brauns, at the Cape of

Good Hope, found *Diplomorium longipenne*, with its enormous ♀, living in this region along with *Messor*, in the manner of our lestobiotic *Solenopsis*, and has so described it.

Many years ago—before 1901—Haviland sent me for the first time the minute worker of *Carebara vidua*, which he took, together with its gigantic ♀, at Natal, in the sub-tropical region of West Africa, in some immense termitaries built by *Termes natalensis;* we have represented both of these in fig. 103. Haviland added in appropriate terms: "you will not be able to believe me, but this ♀ really does belong to the ☿; I took them together, and also their brood, in special chambers of the termitary." I replied to Haviland by return of post: "I have good reason for believing you, as I myself have a similar case, though it is less extreme." I had, indeed, already received from India a very small ☿ belonging to the large *Carebara lignata* ♀, attached to the antennæ of the ♀ in question, which was taken on the wing during its ærial nuptials. The *Carebara* are evidently incapable of transporting the enormous larvæ of their ♀ from one chamber of the nest to another. But there is no need for them to do so. The white, soft and succulent young termites yield them so much white blood to suck that they have only to journey to and fro along their little passages and empty their cropful of this blood into the greedy mouths of their large, motionless female larvæ. And when these larvæ turn into nymphs and are hatched on the same spot, and when their wings and those of the ♂ grow stronger, they can walk out of their prison unaided and fly off with the ♂ towards the blue sky to consummate their nuptials. When they have done thus much, these ♀ shed their wings and invade other termitaries to found more colonies. How this is done, the future must teach us.

It remains only to add that a splendid book entitled

Les Termites, by M. E. Hegh, an industrial engineer, was published in Brussels in September, 1922, and the author sent me a copy. In it he writes as follows:

"According to Dr. Bequaert, a variety of *Carebara*, *Carebara vidua* Sm. r. *Junodi* For., lives in the large termite-mounds in Katanga. At Sankisia, on October 6th, 1911, the observer watched the nuptial flight of this ant; the rainy season was just beginning, and two days previously it had rained heavily. About midday a number of winged females were flying all about the savannah; they emerged from a certain number of termite-mounds, the sides of which were covered with thousands of very small workers of the same species."

All that I predicted above, and had already written in 1920, is therefore confirmed point by point by Dr. Bequaert, with whose observations I was then unacquainted. The fertile ♀ of *Carebara* evidently use their strong mandibles to hew out dwellings for themselves in termite-mounds and there lay their eggs. As soon as they are hatched the small ☿, whose mandibles are no less powerful in proportion, dig minute passages for themselves in the same termite-mound, wherein to devour the young termites and take them as food for their mother and the brood she produces.

Wheeler is doubtless right in thinking that *Erebomyrma*, *Carebarella* and *Tranopelta* of tropical America live in lestobiosis with termites, as they are found in termite-mounds. The following species from the same country also live among termites, and are suspected by Wheeler of lestobiosis: *Monomorium termitobium*, *Heyeri* and *decamerum*, *Solenopsis Schmalzi*, *brevicornis*, etc., *Cremastogaster quadriformis* and *alegrensis*, *Pheidole termitobia*, *Tapinoma Heyeri* and *Brachymyrmex termitophilus*.

The same doubtless obtains with *Aeromyrma nossindambo*,

which lives in Madagascar, and with other *Aeromyrma* and *Oligomyrmex* from India and Africa. Despite the extreme smallness of their ☿, these ants allow themselves the luxury of a ♃, which often has horns on its occiput, but is scarcely larger than the worker, whereas the ♀ is relatively much larger. The genus *Pædalgus*, especially in the species *P. termitolestes* and *Escherichi*, is related to *Carebara*, and lives in lestobiosis with termites. *Bondroitia*, which is totally blind, but whose habits are as yet unknown, must have similar tendencies. I have found certain *Camponotus* (*Myrmorhachis*) in termite-nests.

Whether they live with termites or other ants, these little creatures, which are so many collective synechthrans, are characterized by their trick of stealing and devouring their neighbours' brood. Some of them, as we saw in the case of *Solenopsis fugax*, represent a transition to a more laborious and less parasitic way of living, such as that followed by *S. molesta* of the U.S.A. The little thieves we are now about to describe are much more innocent.

2 Cleptobiosis

I have restricted this term, which Wheeler formerly used also to cover lestobiosis, to the habits of ants which frequently live in double nests for the purpose of exploiting the booty which other and larger ants have hunted or gathered. Chief among these are certain *Dolichoderinæ*, which excel at this art, because it demands special agility, coupled with great impudence. These thieves are not altogether satisfied with eating the refuse of the large ants to which they act as satellites; they plant themselves across their path, and often take them by surprise and compel them to yield up the booty they have won.

Our *Tapinoma erraticum* and the American *Iridomyrmex*

analis, *Forelius McCooki* and *Conomyrma pyramica* are proficient in their art, which I have observed myself, especially in the case of the last-mentioned. According to Wheeler, it prefers to attach itself to the nests of *Pogonomyrmex molefaciens* and *occidentalis*, which do it no harm. While in India in 1891, however, Wroughton saw a large number of *Cremastogaster* lie in wait in the road for some harvesting *Holcomyrmex*, coming home laden with seeds. They threatened the *Holcomyrmex*, and even attacked them, snatched away their burdens and bore them to their own nests.

We have already alluded to similar tactics on the part of *Tapinoma*, *Myrmica*, etc., which climb up grass-blades while the battles of our large European *Formica* are in progress, and take possession of the corpses and cocoons during and after the fighting. This behaviour is related to cleptobiosis. *Iridomyrmex humilis*, *Prenolepis longicornis*, *Plagiolepis longipes* and other ants distinguished for their agility, also practise cleptobiosis in the broader sense of the word, without living in double nests.

Chapter VII

SLAVE-MAKING ANTS

1 *RAPTIFORMICA SANGUINEA* AND RELATED SPECIES

a Europe and Northern Asia. *R. sanguinea*, which we mentioned in Chapters I and III in connection with alliances and wars, is undoubtedly the most intelligent, that is, the most modifiable in its instincts, of all known ants. Chapter II of Part III dealt with the remarkable way in which the fertilized ♀ founds a colony by attacking single-handed a colony of *Serviformica fusca* r. *glebaria* or *S. rufibarbis*. But the cardinal fact distinguishing her is this: although her instincts lead her to steal the nymphs of weaker species in order to make slaves of them, she is at the same time perfectly capable of working on her own account. On occasion she can dispense altogether with these slaves, which are, so to speak, a *luxury* for her; she delegates some of her domestic labours to creatures which she has not taken the trouble to rear, and thus sets herself free to roam about. This aim can hardly be a 'conscious' one in the human sense of the word, but facts speak for themselves, as we shall see.

The term 'slave' drew storms of protest from Huber. Ants have no slaves, he declared, but only 'auxiliaries.' True enough, as we have seen in the experiment on young ants at the beginning of Chapter I, the ant in her nymph-sheath has no knowledge of the companions which have

nursed and cared for her; she has, therefore, no knowledge of her formicary, as we can also tell by Miss Fielde's experiments in Chapter II. Accordingly, ants which are stolen in their nymph-stage are not conscious in any way of being slaves, and work by hereditary instinct. In this sense, Huber is right. But this makes them still less like auxiliaries or voluntary servants; they are 'unconscious slaves,' something like the children born in America of former negro slaves, but they do not think about the fact as some of the negroes were afterwards capable of doing. Hence I will retain the word 'slave,' though these slaves are just as much the masters of their mixed formicary as the species which stole them in their infancy. The only ant which is known to be a real slave-maker, the ravisher of adults, is *Strongylognathus Huberi* r. *alpinus*, as we shall presently learn on the authority of Kutter.

The slave-making expeditions of *R. sanguinea* take place in Switzerland in either the middle of June or the middle of August. They are not common, each formicary limiting its energies to two or three a year. They begin in the morning between about 9 and 11 o'clock, and may last till midday, 1 or 2 p.m., or even later.

To take an example:

At 9 o'clock in the morning on July 14th, 1901, I saw a little troop of *F. sanguinea* leave its nest, situated in a meadow at Chigny, near Morges, and turn off through the grass towards a tree. On coming within 2 metres of the nest this troop hesitated, broke up its ranks to some extent and sent a few 'emissaries' to the nest to call out more ☿. The *sanguinea* then went gradually forward again until they were within about 5 metres of their home, with a second troop of the same kind behind them. Between these two troops, ants were journeying to and fro, tapping one another

sharply with their antennæ, and so it continued: a third troop followed the second, then a fourth, and all sent emissaries back. They followed a tortuous route, and hesitated continually; apparently they were seeking for something, and their advance was very slow. By 10 o'clock they were scarcely 20 metres away from their nest, and the first detachments were becoming indistinct; but the ☿ were still pouring out of the nest in the same direction and forming fresh troops. At about 10-45 this scattered army, which had reached a distance of some 30 metres from the tree and was marching in irregular spurts, turned off at a slight angle and quickened its pace a little. I suspected that it had some aim in view, and on searching I discovered a *S. glebaria* nest situated about 40 metres from that of the *R. sanguinea*. The first marauding ☿ drew near it at about 11-30, and the *glebaria*, taking fright, even made a prisoner of one which had advanced too far. But as soon as the *sanguinea* recognized the nest, they withdrew and ran speedily to arouse the attention of their companions by giving them sharp taps signifying 'Forward, quick march!' When they had come within 4 or 5 metres of the *glebaria*, however, the *sanguinea* stopped and formed a semi-circle round the nest, while numbers of *glebaria* came forth and formed a kind of black cluster round their door. A few of the most prudent or most timorous ☿ could even be seen carrying away some white nymphs. The semi-circle of *sanguinea* then gradually became a whole circle, which left the poor *glebaria* no means of escape; some of them accordingly returned to their nest, which they tried to barricade with earth.

This was the supreme moment—the time of attack; and it occurred at about 12 o'clock. Suddenly the *sanguinea* which were forming the circle sprang, as though at a given

signal, upon the *glebaria* dome. At the same instant, the black cluster became adorned with white flowers, as though by magic, for the *glebaria*, overwhelmed by the *sanguinea*, despite their brave and vigorous resistance, had but one thought left to them—to flee with their white nymphs. But this did not suit the purpose of the *R. sanguinea*: they sprang upon the *glebaria* which were already laden and snatched their nymphs from them; then round the door of the nest they set up a provisional military customs-house, which benevolently allowed every *glebaria* ☿ to pass, if she was not laden, but set its face sternly against the transportation of any nymphs, cocoons or larvæ, as much as to say 'No baggage, ladies!' And straightway the *sanguinea* themselves placed back in the nest all the nymphs they had just taken away from their legitimate possessors. Vainly did these poor creatures strive to bring out more. Yet all this time the thieves did not do the slightest harm to the fertilized *glebaria* ♀ which were escaping, nor to those ☿ which forbore to defend themselves with too much poison and to grip hold of the aggressors' limbs.

While the *glebaria* were escaping to grass-blades with a few nymphs which they had saved, more especially at the beginning of the incident, the chain of *sanguinea* between the two nests was never broken for an instant, and gradually became a more continuous line.

Between 12 and 1 o'clock the *glebaria* were pursued into the grass outside their nest by the *sanguinea*, which then deprived them of most of the nymphs they had saved; they evacuated their nest completely, never to return, and sought other homes with their laying ♀. Then only did the *sanguinea* begin to transport gently to their own nest, one by one, the nymphs and larvæ they had stolen. This removal was continued by a scattered file during the whole of the

next two days. Not until the third day did the *sanguinea* abandon in their turn the old *glebaria* nest, which was then completely deserted. In the mountains and the northern district, *S. fusca* in the strict sense replaces *glebaria* as the slave of *R. sanguinea*.

The case of *Serviformica rufibarbis* is practically the same. Though much quicker and bolder than *S. fusca* and its races, this ant does not offer such a long resistance as *R. sanguinea*, perhaps because its courage, its open nests and its fighting tactics—which are similar to those of the robber, but are counterbalanced by smaller stature, less strength and above all, less rapidity and power of combination in obeying mutual signals—enable it to be nonplussed more quickly than an ant which resists in a different way. In Chapter III, we saw how this same *R. sanguinea* was completely routed by a few *P. rufescens* whose courage, strategy and unity of action greatly surpassed their own. In a word, no sooner do the *rufibarbis* recognize any *sanguinea* which have just arrived than they come out of their nest in crowds and attack them furiously. The *sanguinea*, however, hasten to encircle them and begin their assault. The chaos of the fight is indescribable, but so great is the terror of the *rufibarbis* that they come out almost immediately with their nymphs through the numerous openings of their nest. The precision of the *sanguinea* assault is incredible. Without losing a moment, they take possession of all the doors and there install their customs-house, snatch away the nymphs from the *rufibarbis*, sending back to the nest all the ☿ which carry the young, and then pursue them and turn them out everywhere. A few *rufibarbis* ☿ return alone to the nest with the courage of despair, and try to rescue nymphs, but they are scarcely ever successful; the customs-house is too efficient. In short, all is over much more quickly than in

the case of *glebaria*. I once saw some *sanguinea* attack on the same day, one after the other, two *rufibarbis* formicaries 7 metres apart.

In Europe and throughout the palearctic fauna, *R. sanguinea* constitutes but a single race without any appreciable varieties, extending from Italy to Scandinavia and from England to Japan. Yet there are a remarkable number of variations in its habits. Some formicaries have as many slaves as masters, whilst others, somewhat rarely encountered, have none at all. I observed this fact chiefly in the mountains, but also on the plains. Some time ago, I came to the conclusion that the *sanguinea* with no slaves have a special abundance of very small workers. This ant often has two or three nests, and changes its quarters from one to the other. In 1910, at the Chalet Boverat in the Jorat (Vaud), I made the following observation:

While seated near a *R. sanguinea* nest, I wished to show someone the slaves, but could find none. Wishing to demonstrate the robbing of the *S. glebaria*, at any rate, I wandered for 100 metres, also in vain, seeking this species. The meadow in which the nest was situated was surrounded on three sides by a pine-forest. As I came back on the other side, I discovered more than forty *R. sanguinea* nests in succession, from 2 to 5 metres away from one another, all absolutely free of slaves but with ☿ of small stature, forming a single polycalic colony over the area given above. I put some ☿ together from the nests most widely separated and the result was immediate friendship. I examined a much wider area still, and all in vain: there was no trace of *S. glebaria* or *rufibarbis*. Such a thing was then absolutely new and exceptional. In explanation, I can only offer the following conjecture: as the forest surrounded the meadow on three sides, the *sanguinea* had plundered all

the *glebaria* nests within reach and thus gradually driven out their inhabitants, after which they ceased to make slaves. On the other hand, they had all the better opportunity of increasing the number of their nests, as the isolation of the meadow caused their fertilized ♀ to return. Moreover, the inadequate feeding of the brood resulting from the lack of slaves must have caused the diminution in their stature, as it usually does in such a case. I offer this hypothesis for what it is worth, until it is supplanted by a better one.

However that may be, we find in Europe all kinds of transitions—*R. sanguinea* with half their formicary consisting of slaves, others with a smaller and smaller proportion of slaves, and yet other exceptional ones without any at all. According to Wasmann's statistics, the average number of slaves diminishes in proportion to the increase in the population of the formicary. Furthermore, it is not uncommon to find *R. sanguinea* formicaries, which, unlike those of *Polyergus*, possess two kinds of slaves at the same time, *glebaria* and *rufibarbis*. Finally, in Chapter I, sections 3 and 4, we have seen two cases showing that *R. sanguinea* after a victorious battle with *F. pratensis*, even in the natural state, will sometimes rear the nymphs and thus provide itself with *pratensis* slaves, as in the artificial combats induced by myself. Wasmann has made similar observations. A *sanguinea* formicary stole the cocoons of a small, natural *pratensis* formicary. But as soon as they were hatched, the *pratensis* went foraging and discovered their mother; they then carried her back to the nest to replace the ♀ of the *sanguinea*, which had been lost. In this way the *sanguinea* colony gradually became a *pratensis* colony.

In 1898 I established a colony of *R. sanguinea* in a glass-covered apparatus and gave these ants the nymphs of several species. I succeeded in making them rear and adopt

the following: *Serviformica glebaria*, *rufibarbis*, *cinerea*, *Formica pratensis*, *rufa*, *exsecta* and *pressilabris* (☿) as well as *Polyergus rufescens* ☿ and ♂. The *F. exsecta* and *fusca* were distinguished by their activity in working, the *Polyergus* by their complete idleness, the *sanguinea* by their skill, and the *pratensis* by their clumsiness. On the other hand the *sanguinea* killed all the ♀ and ♂ nymphs of the other species, often under my very eyes, and took care that only the ☿ nymphs were hatched, whereas the *Polyergus* ♂ were reared by some *exsecta* or *glebaria*. At the same time the *sanguinea* reared some larvæ of *Lomechusa* (a beetle guest; see Part II, Chapter IV) to which they disgorged honey-dew, though instead of rearing the nymphs of *Lasius*, *Dendrolasius* and *Tetramorium* which I gave them, they ate them all. They took great care, however, in the rearing of their own ♀ and ♂, whose flight to their nuptials on a small artificial islet, attached to my apparatus, I was able to observe.

I have often brought about an artificial fight by setting a handful of *R. sanguinea* upon a colony of *S. rufibarbis*. As in the natural invasions, these few were enough to drive the *rufibarbis* from their nests, and were able to storm their holes, etc. On one occasion a few bold *sanguinea* succeeded in putting a large *rufibarbis* colony to flight, but at the same time they were so mauled by their enemies in the field that they could neither make an onslaught upon them nor set up a 'customs-house.' The *rufibarbis* then recovered from their initial fear, forced the fugitive *sanguinea* to return and killed them all.

Small troops of *R. sanguinea* also frequently attack the nests of *Lasius niger* and *flavus*; they amuse themselves by killing the inhabitants and carrying off the nymphs, but only in order to eat them and incidentally to establish

themselves in their nest. On the whole, it is the slaves of the mixed *R. sanguinea* formicaries which play the chief part in tending the young and milking aphids.

b America. Although the Old World possesses only *R. sanguinea* proper, Wheeler has counted no less than eight kindred varieties, races and species of this same *Raptiformica sanguinea*, and no less than fourteen varieties, races or species which they use as slaves. For the sake of simplicity, we will mention each of these only by the name of its variety or race.

The slave-making forms are *R. aserva*, *rubicunda*, *subnuda*, *subintegra*, *puberula*, *obtusopilosa*, *Pergandei* and *munda*, the two last being species. Neither *munda* nor *aserva* has slaves.

The slave-forms belong to two groups, that is, two typical species, with races and varieties. The first consists of the European *Serviformica fusca* and its American races and varieties *subsericea*, *glacialis*, *subænescens*, *neorufibarbis*, *neogagates*, *argentata*, *subpolita*, *neocinerea* and *neoclara*. The second group is exclusively American, and includes *Neoformica pallide-fulva* with its races and varieties *Schaufussi*, *nitidiventris*, *incerta* and *fuscata*.

In 1900, I myself discovered in the park at Toronto the race *aserva*, with its slightly indented epistoma, forming a large polycalic colony entirely free of slaves, exactly like that of the Chalet Boverat in the Jorat, as mentioned above. In 1910, I was struck by this similarity, and by the absence of slaves in both cases. But in 1900, I at once placed a handful of *S. subsericea* with their brood near the *aserva*, which pillaged the nymphs exactly as our *sanguinea* do. Unlike the *sanguinea* of the Chalet Boverat, however, the *subsericea* were very abundant in the region in question, and it could not have been their fault that no plundering expeditions took place. The *aserva*, moreover, were big and

strong, and by no means stunted. At a later date Wheeler confirmed my observations, and the fact that *R. aserva* never makes slaves. He proved, on the other hand, that the fertilized ♀ of this American race founds her nest, as do the other races of *R. sanguinea*, by stealing singlehanded the nymphs of *S. glacialis*. But this instinct is not inherited by the worker, which only possesses it in a latent form, as my experiment has just shown: the *aserva* ☿ must, therefore, have entirely re-adapted themselves to a complete working routine. The exception of the Chalet Boverat has become, in their case, the rule of instinct. You will agree with me, dear reader, that it is interesting to compare the re-awakening of the slave-making instinct, recently latent (as shown in my experiment in the park at Toronto) with that of *Strongylognathus testaceus* (as quoted in Part III, Chapter VII) which has already brought about the partial extinction of the worker.

The American *Raptiformica* varies a great deal in its choice of slaves, which also depends, for that matter, on the local fauna. Wheeler mentions as slave-species:

1 Of *R. rubicunda: S. subsericea*, *neorufibarbis*, *subænescens*, *neogagates* and *N. fuscata*.

2 Of *R. subnuda: S. subsericea* and *argentata*.

3 *R. subintegra: S. subsericea*, *glacialis*, *subpolita*, *subænescens* and *neogagates;* also *N. Schaufussi*, *incerta*, *nitidiventris* and *fuscata*.

4 Of *R. puberula: S. subsericea*, *argentata*, *subpolita*, *neocinerea*, *neoclara* and *neogagates*.

5 Of *R. obtusopilosa: S. argentata*.

6 Of *R. Pergandei: S. subpolita* and *N. pallide-fulva*.

Wheeler has also found two and even three kinds of slaves in the same *Raptiformica* formicary. In a Colorado meadow, for instance, he found *S. neoclara*, *neocinerea* and

N. nitidiventris as slaves in one formicary, and in practically equal proportions.

In short, the American *Raptiformica* makes more slaves than the European *sanguinea*, although the number also varies a good deal. In Connecticut and other places, I was interested to find that the numbers of the big *subsericea* slaves in an average *R. rubicunda* colony were larger than those of their masters. I once saw a natural expedition undertaken by a small number of *rubicunda* against a colony of *subsericea* which were much more numerous, and some of which were much larger than themselves. It was scarcely any more than a pleasure-party. There was no need to besiege or encircle the *subsericea*, for they did nothing but decamp as soon as they caught sight of the enemy. The *rubicunda* had only to guard the doors and remove the cocoons to their own home; the time of day was the same as in Europe.

Wheeler confirms my observation that the slave-ants of America do not defend themselves so well as those of Europe. He gives us the following particulars of a raid by *R. rubicunda*, which he observed at Rockford, in connection with a colony of *N. fuscata*, a powerful subterranean race. About 400 *rubicunda* from the army stopped round the opening of the *N. fuscata* nests and made alternative advancing and retreating movements, encircling the nest as they did so, as though they were afraid of the *fuscata*, which, however, scarcely showed themselves. But after half an hour or more the *rubicunda* became more daring; they began to invade the nest and bring out larvæ and nymphs. Finally at 4-35 p.m., after they had completed their circle, a winged ♀ of *N. fuscata*, followed by fifty others, and a crowd of workers laden with larvæ and nymphs, poured out of the nest-opening. They spread in every

direction, breaking the chain of *rubicunda* and climbing with their long legs on to the grass. But in an instant the *rubicunda* fell upon them all and snatched away their nymphs; only a few were saved by the ☿. Ten minutes after the exit of the first winged ♀, all the *fuscata* had fled, and the *rubicunda* began to move the brood to their own nest, 40 metres away. This nest contained a large number of *S. subsericea* slaves and very few of *N. fuscata*. By 5-30 p.m. the transport of the captured brood had been completed. The *fuscata* took up their abode under some leaves, 2 metres distant from their old nest. Not a single ant had been killed on either side.

According to Wheeler, *subsericea* resists *R. rubicunda* better than the *pallide-fulva* group. He saw a raid carried out by *R. rubicunda*, according to all its usual rules, against a colony of *Myrmica scabrinodis* and one carried out by *R. subintegra* against some *Lasius americanus*. Both aggressors stole their enemies' nymphs and carried them to their own homes, evidently intending to use them as food, as our own species do.

2 *POLYERGUS* OR AMAZON ANTS

a Europe. In my book on the Ants of Switzerland, I have devoted nearly thirty large pages to the habits and expeditions of *Polyergus rufescens*. As I do not wish to repeat myself here, I will refer you to that book, dear reader (*Les Fourmis de la Suisse*, now in its second edition). All my old observations, experiments and statistics are still perfectly exact, and I will content myself here with summarizing the facts, which are unique of their kind. In Chapter III we have already described the tactics of *Polyergus* in its wars against ants of its own and other species, particularly *R. sanguinea*; Chapter II of Part III explained,

on the authority of Emery, how these ants found their colonies in Europe, and develop them after the initial stages. In this connection we have mentioned their scouts, which go forth alone to spy out the nests of their future slaves. In Europe, these are invariably either *S. glebaria* or *S. rufibarbis*, never both together in the natural state. As *P. rufescens* is not found in our mountain and woodland region, I have never, strictly speaking, seen it using *S. fusca* as its slave.

Polyergus rufescens is 6·5 millimetres long on an average, and its colour is a dull, uniform reddish-brown, which becomes more yellowish and shiny in the *ergatogynes* (see Part I, Plate I), and the largest ♀; its chitin is hard and tough, and its recumbent topochemical organs well developed. I suppose they enable it to perceive the odour of the subterranean *S. glebaria* nests, which it probes with its antennæ in a very persistent manner during its reconnoitring expeditions. Fig. 106 *C* shows its curved, toothless mandibles, expressly designed to pierce the brain of an enemy, as shown in figs. 106 *B* and 106 *C* (see below), thereby paralysing its mandibles, as I have proved, and to carry the stolen nymphs or cocoons whose shells they compress slightly as they hold them between their legs (see fig. 106 *A*). My readers are requested to compare these mandibles with the very similar ones of *Strongylognathus testaceus*, shown in fig. 104. The habits of this curious parasitic ant were described in Chapter VII of Part III, and we shall shortly deal with its congeners from which it has inherited these mandibles by phylogeny.

The body of *Polyergus*, therefore, already betrays the fact that its instincts are fixed by heredity. This is not so with *Raptiformica*, on whose body the slave-making faculty has barely begun to set its seal in the slight indentation

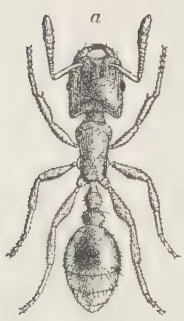


Fig. 104

of the epistoma. The *Polyergus* vary a good deal in their habits, which possess only a few characteristics modifiable according to circumstances. *They have entirely lost the natural instinct of eating without assistance.* This was proved by Huber and re-proved by myself, and our experiments are conclusive. *Polyergus* ☿ will let themselves die of hunger even though the most tempting honey and tasty meat is left close to them for several days. It is amusing to watch them beg their companions in vain for regurgitation, for not one of them is capable of such a thing. They also absolutely neglect all their brood, and are ignorant of the building-art: without their slaves they are helpless. Hence they live in complete dependence upon their auxiliary ants. But if only we introduce a single slave ☿ into the cage where a collection of *Polyergus* has been left in this deplorable plight for two or three days, the scene is changed in a few moments. First of all the slave crams her crop with honey; then the *Polyergus* assail her, to obtain regurgitation, and she immediately complies with their requests. She next gathers the brood together and feeds it likewise, after which she builds a chamber for them all. In less than an hour everything is in order. The loss of all these instincts is undoubtedly singular, and proves an old slave-making phylogeny, whose direct transitions are lacking—at any rate, those between the *Raptiformica* and *Polyergus* of the present day.

The above facts provide the key, moreover, to the frantic courage displayed by these ants: 'Death or victory' is their real instinctive sentiment, without any of the humbug with which it is so often associated in the human sphere.

If an army of *Polyergus* were defeated and dispersed outside its nest, and had no power to return, it would be condemned to starvation. Some *Polyergus* ☿ which I placed in front of the nest of large *Camponotus ligniperdus* attacked these enemies, despite their size and numbers, and allowed themselves to be beheaded without retreating a millimetre. No *Polyergus* ever runs away. Its curved mandibles prevent it, furthermore, from clinging to the legs of large enemies. It always fights its adversary face to face, or rather 'mandible to body,' especially 'to head.'

We come now to the expeditions of *P. rufescens*, and we will begin with the amazons which enslave *S. glebaria*, for they are typical. The differences found in those which have *S. rufibarbis* slaves will afterwards be pointed out.

TIME OF DEPARTURE. *Polyergus* never sets out in the morning, but only in the afternoon, generally between 2 and 5 o'clock. By 7 the troop has always returned. The time of departure depends to some extent on temperature. In chilly weather they start earlier, in warm weather, later; at any rate this usually the case. They rarely go out when the temperature is less than 20 degrees Centigrade.

EXPEDITION-SEASON. In the basin of Lake Leman, it begins at the end of June at the earliest and ends at the beginning of September; it nearly always takes place in July and August.

ENUMERATION OF THE ARMY. I have counted several amazon armies on their return by obstructing the doors of the nests they were invading and only allowing them to return one by one. In this way I have counted between 375 and 1,400 amazon ☿ to an army—if such idle warriors can be described as 'workers.' But there may certainly be as many as 2,000, and in some cases there are separate corps, each of which includes scarcely a hundred

Polyergus. On no occasion, however, does the whole army go out together; as a rule it consists of the majority of the amazons of the formicary, but sometimes of a minority only.

MARCHING-SPEED OF THE ARMY; ITS LENGTH. This depends entirely upon the difficulties presented by the road (thickness of the plants growing in the turf, stones, wind), on the temperature, and on the exactness of their knowledge concerning the aim they have in view. On the outward journey, along some road or gravel path, I have seen an army that is sure of its way run a metre in 26½ seconds; but in thick grass it sometimes takes a minute to do as much. When it returns, laden with nymphs, the same army often takes 1½ minutes to cover a metre. If a man were to move at such a pace, increased proportionally to his size, he would be walking as fast as a railway-train of average speed. When it goes forth, every amazon army has a van and a rear. Between three and eight or sometimes ten ants march in front, and the whole army, from head to tail, may cover 1 to 3 metres, according to circumstances, or sometimes even more.

DEPARTURE SIGNAL. Before the departure, a growing number of *Polyergus* may be seen walking about on their dome, which they do not do in the morning. Suddenly a few ☿ will rush back to the nest and give the signal for departure by striking their companions' foreheads, and the army, ever compact, sets off in some direction determined by various factors. Sometimes the aim is to reach a nest already plundered the previous day, but as a rule all guidance is left in the hands of scouts which have been out ever since the spring exploring the *S. glebaria* nests in the neighbourhood, and whose activities we described in connection with the foundation of colonies. It is evidently they

that lead the army in the desired direction, forming the leading file in a column of 3-8.

ORGANIZATION OF THE ARMY. As Huber has shown, the van of an army, consisting of a few ☿, moves rapidly but is continually renewed, as those in front turn about and tap with their foreheads all the ants they meet, as far as the extreme rear of the legion they are directing. There are no chieftains, but several guiding spirits, which had doubtless been scouts. When the majority knows where it is going, things begin to move rapidly, and it almost seems at first as though an instructive and mysterious impulse is urging them on. But this is by no means invariably the case, as we shall see.

And now, having set out at 4 p.m., our army is on the march with a front that varies every moment; the last ☿, which are, say, $2\frac{1}{2}$ metres behind, bring up the rear and abandon the nest. It would be hard to imagine a more curious spectacle than an army of amazon ants marching thus at top speed towards a goal which is known to some of them only, and unknown to all men who have not studied their habits. It is impressive to watch, and quite different from the procedure of the squads of *R. sanguinea*.

HALTS AND RECONNOITRING. Suddenly the van comes to a standstill. The ☿ scatter in all directions, and seem to be unable to find their way any longer. In a few minutes, however, a small number of ☿ fling themselves in between the others, strike them on the forehead and continue in the direction previously taken, followed by the whole army. Nevertheless, on coming within 35 metres of its nest, the army stops again, and this time the halt lasts for a long time. The whole army keeps together in one mass, and every little while there is a movement in the centre, and one cluster of ants sets off in one direction, another in a different

direction; but in a short time, the ants in these clusters probe the ground with their antennæ, and describe curves back to the centre. In a quarter of an hour's time, the whole army sets off again and returns empty-handed to its nest, without finding anything. The indecision of the ☿ in reconnoitring a nest of *S. glebaria* is obvious; the scouts have lost their compass, that is, their topochemical memory. On reaching its nest, however, the whole army passes over the dome without a pause, and this time heads in the opposite direction, climbs a steep slope in the grass at about 5 o'clock and advances in a straight line, making only one or two slight pauses on the way. Sixty metres from the nest, the amazons slacken their pace and show evident signs of fatigue. Yet right in front of them, I discover, is a fine nest of *S. glebaria*. None the less, the ants have exhausted their strength, and they halt three paces away from this nest (6 metres from their own). Without the slightest hesitation as to the direction to be followed, and without a single ☿ leaving their ranks, the amazons begin their return journey; the van of the army ceases to advance and there follows a general turn-about, due this time not to indecision as to the correct road, but to fatigue and the lateness of the hour. Toiling slowly and awkwardly along, after covering 196 metres or 240 of my paces in three hours without any result, the whole army does not actually return until 7 o'clock. These pauses of indecision and empty-handed returns are not at all uncommon, but I have never seen another case which betrayed so clearly the effects of fatigue and the lateness of the hour.

ATTACK. An amazon army which yesterday returned home empty-handed, after many fruitless investigations, sets out in the same direction at 4 o'clock, but this time without hesitating, and continually inclining a little to the

Formica pratensis ejaculating poison at an approaching man.

Formula brevium elucidatur horizon et sui subscripti mem.

fol. XII.

fol. II. ov

right through a cornfield, which, as I now surmise, must have baffled them the day before. On leaving the cornfield, it comes straight upon a large nest of *S. glebaria*, which it immediately invades through an open gallery. Soon a few *glebaria* climb up grass-blades with their cocoons. The amazons then rush out again laden with prey, and return home in fairly good order, only the last being attacked and chased by the *glebaria*, which have come out and recovered from their surprise. At 4-45 p.m., when the amazon army returns to its nest, it does not enter it again, but lays down the stolen nymphs in heaps before one of its doors, leaving to its slaves the task of placing them in the nest; it at once sets off again for the plundered formicary, and passes alongside those which are still coming back laden with spoils, without crossing their path or causing disorder. Meantime, the *glebaria* have barricaded their doors with grains of earth, and when the head of the amazon army again reaches their nest it waits for a moment, then clears away the grains of earth and pours once more into the nest without any effort, jostling its defenders which flee with a few nymphs. This time the amazons return home laden with riches which they themselves take into their nest. Rarely have I found a *Polyergus* ☿ dead or half-dead in a *glebaria* nest.

RETURN. On the return journey, the laden amazons march in much less serried formation and a little slower than they did on the way out, but they never halt. Fig. 105 (after André), represents the return of the rear of an amazon army laden with cocoons; the disconsolate *glebaria* can be seen behind. As shown in fig. 106 *A*, the *Polyergus* bear the stolen nymphs between their legs, and this enables them to run faster. The slaves (fig. 106 *C*) pinch one end of the shell. One very amusing result of this instinct is the fact that the amazons are incapable of carrying the cocoons of

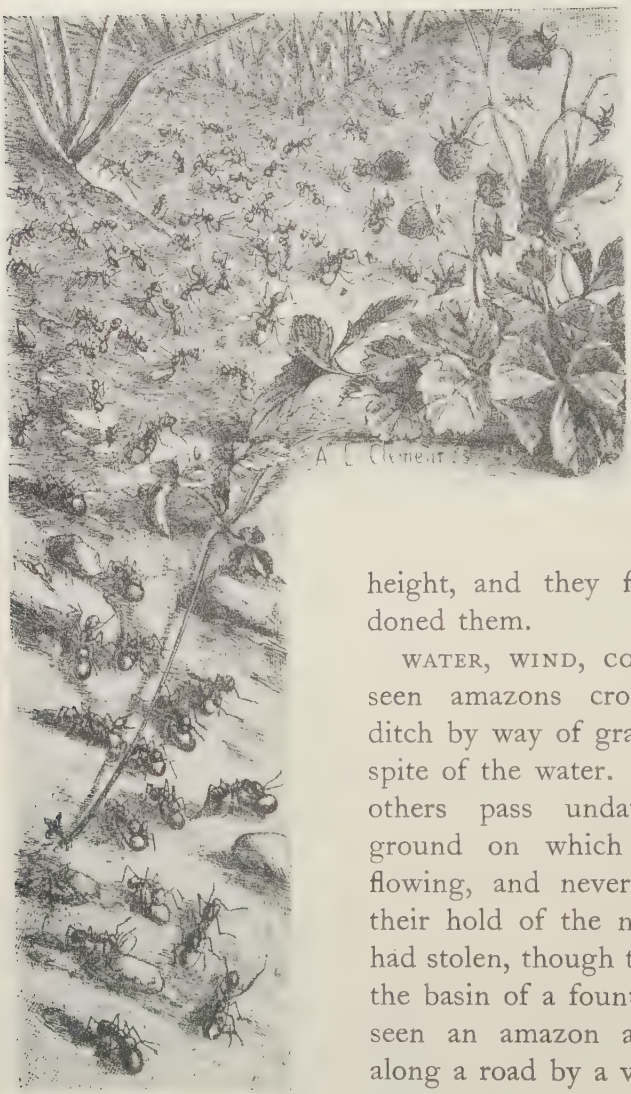


Fig. 105

the *glebaria* ♂ or ♀. I have seen them struggling in vain to get astride of these large cocoons; their legs were too short to reach the ground from that height, and they finally abandoned them.

WATER, WIND, COLD. I have seen amazons cross a small ditch by way of grass-blades in spite of the water. I have seen others pass undaunted over ground on which water was flowing, and never even relax their hold of the nymphs they had stolen, though they fell into the basin of a fountain. I have seen an amazon army, swept along a road by a violent wind, climb back up the road in the face of the wind and dust, in order to attack a formicary on the other side. *Polyergus* is paralysed by the cold. At

5 o'clock on September 5th, some amazons were standing in a motionless mass on their dome, when a few ☿ gave a faint departure-signal. Scarcely one-fifth of the army followed this movement. Twenty paces away from the nest the shade of a cherry-tree benumbed the *Polyergus* and stayed their march, so that the whole army remained absolutely motionless for five minutes; it then turned about and went back very slowly to its nest. It has been claimed that ants can always foretell rain, but this is inaccurate. I have seen *P. rufescens* and *R. sanguinea* absolutely surprised and checked during an expedition by reason of a rain-storm.

SUBTERRANEAN NESTS. An amazon army comes within twenty paces of its nest and stops. But in this case the ☿ do not seek for their road and do not scatter; they probe the ground attentively with the topochemical organs in their antennæ, and hunt among the grass-tufts. At length there is a motion in the direction of a hole smaller than a hemp-seed, into which the amazons pour one by one. But this takes overmuch time; suddenly a thick tuft of grass, 3 decimetres away from the hole, is invaded by the army, which gradually disappears into it; it must, therefore, have concealed an opening. Then nothing happens for five minutes. There are only one or two *glebaria* strolling about on the grass. At last an amazon comes out of the grass-tuft bearing a cocoon, and then a complete file follow her one by one, laden in the same way. A second file of the same kind then emerge from the first hole, which is visible from the outside. The two files unite and return to the *Polyergus* nest, but so slowly that some ☿ are still coming out of the invaded subterranean nest while the first ones are already back on their dome. All of them are laden, so that the domeless subterranean nests cannot always be sparsely populated.

I should never come to an end if I tried to tell you all the details of amazon expeditions. Sometimes the army divides into two corps, one of which attacks one nest and the other a second nest; sometimes it completes two and even three expeditions in one afternoon; sometimes one section, seeking its road in vain, loses heart and returns home, while the other perseveres and finally succeeds in discovering a *S. glebaria* nest, which it plunders. I have also seen an army which has stopped through indecision, halfway along its road, suddenly turn off at an angle from the direction it had been following and eventually find a nest in the second direction. In this case it follows the same angle over again when it returns, and is not able to return in a straight line except when it is in the immediate vicinity of its nest.

AMAZONS WITH RUFIBARBIS SLAVES. The nests of *S. rufibarbis* always have several large holes. Although *S. glebaria*, or its variety *rubescens*, which amounts to the same thing, are found in the same climate as *S. rufibarbis*, I have never seen a single natural amazon formicary take both these ants as slaves, and I had great difficulty in causing them to do it artificially. An amazon army marches in more serried and compact ranks against *rufibarbis* than against *glebaria*. Let us consider its method of attack. On coming within a decimetre of a *rufibarbis* nest, the van of an army catches sight of it, stops abruptly and sends out a crowd of emissaries which hasten to the rear. "We are there: forward!" In less than thirty seconds the army is assembled in one mass before the enemy nest, and in a second movement of unparalleled impetuosity the entire company is hurled on to the dome. The attack coincides with the recognition of the thieves by the *rufibarbis*, and these within a few seconds cover their dome with defenders. An indescribable melée

Fig. 106 A and B

follows: the amazons rush through all the openings into the galleries of the nest, and at the same moment the *rufibarbis* come flooding through the same orifices in hundreds,

bearing their brood. But in this case, the amazons remain in the nest scarcely more than a minute and come out in fairly close ranks through all the holes, laden with nymphs. The scene then changes. Seeing that the thieves are escaping, the *rufibarbis* pursue them in a rage, seize them by the legs and try to recover the stolen cocoons. When one of them takes hold of a cocoon, the amazon will slide her mandibles along it until they reach the head of the *rufibarbis*, which usually relaxes her hold; otherwise her head is caught

Fig. 106 C

between the two hooks, and if she still refuses to give way, her brain is mercilessly pierced, as shown in figs. 106 *B* and *C*. I have seen one or two cases in which the mandibles of the *rufibarbis* thus done to death had not let go of the cocoon, which was borne away by the amazon along with the corpse. If a laden amazon is held by a leg she does the same thing, but in this case she is always obliged to release her cocoon in order to threaten or destroy the *rufibarbis*.

Sometimes a companion *rufibarbis* will then arrive on the scene, and hastens to take up the cocoon under the amazon's nose. This state of affairs is represented in fig. 106 *A*, the seizure of a leg; *B*, the execution and the arrival of another *rufibarbis*; *C*, the first *rufibarbis* lying dead while the other runs off with the cocoon. In fig. *B* the artist has erroneously removed the right middle leg of the *Polyergus*.

Sometimes the amazons carry off young, freshly-hatched *rufibarbis* instead of nymphs, and their victims accept their lot. The last amazons, wrathfully pursued sometimes to a distance of 10 or 20 metres from the *rufibarbis* nest, strive to return to the nest to recover the cocoons which have been snatched away from them, but they rarely succeed and must be considered fortunate if they return safe and sound, which they cannot do without killing a few enemies. Some of them, though not many, are even seized by five or six *rufibarbis* at the same time, drenched with poison and killed. Others busy themselves with delivering their companions which have been seized by a leg, but as a rule they all run home in haste. It is apparent that these combats are infinitely more deadly, especially for the *rufibarbis*, than those with the *glebaria*.

A few more special cases are worthy of mention:

When the fertile ♀ die, their places are taken by the *ergatogynes* (Vol. I, Plate III, fig. 3). I once saw some amazons form a front several times in one afternoon, but never venture further than two or three of my paces from their nest. They turned back on each occasion and no real expedition took place that day. At other times I have seen amazons walking round and round their nests instead of going on expeditions.

Twice in succession I saw a number of amazon ♀, some still with their wings, set out on an expedition with the army

of ☿; but they frequently stopped, so that they were soon well in the rear. On one occasion, however, some of them succeeded in mounting the dome of the *rufibarbis* which were being attacked, but they were unable either to enter the nest or to carry off cocoons; they contented themselves with fighting the *rufibarbis* furiously and killing many of them. When the army returned, these ♀ made no effort to go back with it, but continued to fight alone. A great deal might be said about this aberration of instinct.

One day, an amazon army on the march in thick grass divided and formed two fronts, one of which obtained but few followers and went off obliquely to the left leaving the main body, now the poorer by less than a hundred ants, to continue on the right and plunder a large *rufibarbis* nest. The small troop showed no anxiety on account of its scant following, though the emissaries which it sent out found scarcely a single recruit, but after a moment's hesitation fell upon an enormous nest of *rufibarbis*, and in spite of the angry host of defenders, found its way into the nest. A few amazons even succeeded in stealing nymphs, but their thefts were so few and far between that the *rufibarbis* did not get wind of their homeward direction, and were incapable of pursuing them. Perceiving their adversaries' weakness, moreover, the *rufibarbis* removed very few of their nymphs, and soon brought them back. The surprise attack was so short that the *rufibarbis* only took two or three amazon prisoners.

On one occasion an amazon army probed the ground for an hour before finding a spot in which the ☿ could dig a hole leading to a subterranean nest which they plundered.

At the end of June I saw some amazons preparing for their expeditions by making a few outlets round their nest. The slaves seemed to be surprised at this and seized

them by the mandibles to bring them back to the nest, but they afterwards grew accustomed to the expeditions and paid no attention to them.

I have often poured out a bagful of *glebaria* or other cocoons before an army of *Polyergus*. Supposing, doubtless, that there was a nest hard by, the amazons would waste their time digging in the earth instead of taking the cocoons which were near at hand. Rarely did they carry off one of these. Here we can realize the blindness, or in plain words, the stupidity of fixed instincts, and also the superiority of the intelligence shown by *R. sanguinea* over the fixed instincts of *Polyergus*.

One fine day an amazon army marched to a nest of *S. rufibarbis* which had just been pillaged by some *R. sanguinea*. The *Polyergus* overthrew the *sanguinea* instead of the *rufibarbis*; but there was nothing left to take as the *sanguinea* had already removed all the booty; the second robber was robbed.

We have already mentioned the insane fury displayed by the amazons when fighting *R. sanguinea* or *F. pratensis* or else their fellow-creatures from other formicaries. At such times they bite everything—cocoons, pieces of wood, even their *glebaria* slaves which try to calm them, or their own companions, and can no longer recognize the way they have to go. However, when the enemy has departed, those which have survived gradually recover their senses and their mental equilibrium, cease to bite without good cause, and eventually find their path again.

In 1869 I placed an amazon formicary in an apparatus and carried out a number of experiments with it. I have already described the battle which took place between these ants and other amazons, and also the shameful defeat which sixty of them inflicted upon a large *R. sanguinea* formicary.

At Zurich I even succeeded in making my amazons attack a nest of *F. cinereo-rufibarbis*. But the most curious incident of all was the following, which took place in 1873 when I had given my captive formicary its freedom and was watching its scouts travel from thirty to fifty paces away from their nest.

The weather had been very hot and dry. Being short of food and plagued by their masters' importunate demands for regurgitation, the *glebaria* slaves were seized with fits of individual impatience bordering on revolt. They began to take hold of the amazons by the legs, bite them and carry them outside the nest to as great a distance as possible, even to threaten them by curling back their abdomens. The amazons endured this treatment so long as it was not pushed beyond a certain limit, for they were too tough to be injured by it. No sooner had an amazon been transported by a *glebaria* some distance from the nest, than back she would come the quicker of the two, as in the case of *Leptothorax* mentioned in Chapter I. But when the *glebaria* began to be too obstinate or too violent, the impatient amazon would curve back her body and take hold of the slaves' head between her mandibles. As a rule the *glebaria* would immediately relax her hold. Some of them, however, grew more and more stubborn and continued to bite. *The amazons then pierced their brains and killed them like so many enemies*. I saw one amazon being dragged about by six or seven *glebaria*, of which she freed herself by killing one. These affairs had degenerated into veritable cold-blooded fighting. Presently the rain began to fall and all these scenes of revolt came to an end. It must be admitted that such facts are very curious, and provide us with matter for reflection and comparison.

In conclusion, I should like to quote here a remarkable

observation by P. Huber, which, to my knowledge, has never been repeated since—that is, in the last 115 years:

"A mixed formicary had been recently established on the terrace of the house in which I lived. I carefully observed the excursions of the amazons, and one day I noticed that they were making for a deserted formicary: the ants which had previously occupied it had no doubt been robbed too often by their formidable enemies and had departed, bag and baggage. The amazons, which were probably not comfortable in their dwelling, took advantage of this circumstance. When they had visited the empty formicary, they retraced their steps, took up in their mouths the ash-black ants (*glebaria*) of the mixed colony and transported them to the other nest. This performance occupied a few hours, and a complete emigration was effected. Thus I saw the opposite of what I had previously found; but I have never had the opportunity of seeing it again. The amazons carried the black ants just as they are usually carried by them. When the slaves were transferred to their new dwelling they remained there, and each species began again to perform its usual functions.

From all these facts we can deduce an important truth relative to the moral sense of these insects, namely, that their instincts are susceptible to some modification. Ants captured in their youth may be tamed and adapted to live with enemy species; it is during the first days of their life, therefore, that the impressions which they will always retain are formed. Objects which would naturally have aroused their hatred will then no longer inspire in them any other sentiment than love."

b America and Japan. 1. polyergus breviceps. This species is closely related to *P. rufescens* of Europe and has

the same dull reddish-brown colouring, but a shorter head. It is found in the Western United States, Colorado and New Mexico, at a height of 2,000-2,500 metres. According to Wheeler, who observed its forays, it reduces *S. subsericea*, *argentata* and *neocinerea* to slavery. Wheeler had counted 1,000 ☿ to one of its armies. Its expeditions are identical with those of *P. rufescens*, but the *subsericea* do not even try to defend themselves, and the "courteous and considerate" *breviceps*, as Wheeler calls them, very graciously content themselves with stealing their brood. The *P. breviceps* set out early in the afternoon. Wheeler has sometimes seen them make a mistake and grasp adult *subsericea* ☿ instead of cocoons, afterwards leaving them quite unharmed a few centimetres away from the invaded nest. No *subsericea* are killed or wounded in these expeditions. They do not even leave their nest.

2. POLYERGUS BICOLOR. This small amazon is red with a black abdomen. It lives in Wisconsin and Illinois, and enslaves *S. subænescens*, making its nest not in the earth but in the fallen tree trunks or stumps found in forests. It seems to me that these expeditions observed by Wheeler bear a very close resemblance to those conducted by *P. rufescens* against *S. rufibarbis*. Wheeler has seen the *P. bicolor* bite the *subænescens* and even the wood with an insensate fury such as I observed in our own *P. rufescens*. The *subænescens* defend themselves valiantly; they do not seem to pursue the *P. bicolor* when they return, but the amazons frequently pierce their heads. Wheeler describes, among others, an expedition carried out by some *P. bicolor* living in a branch of a dead tree against a formicary of *S. subænescens* housed in the trunk of an overthrown tree. The ☿ scouts of *P. bicolor* often disappear under dry leaves and hunt in the earth for *S. subænescens* nests. Wheeler has

also seen forays which failed, and from which the *bicolor* returned empty-handed.

3. POLYERGUS LUCIDUS. This large amazon lives in the Eastern United States and makes slaves of the *Neoformica* of the *pallide-fulva* group. Like these, it is longer in build than the other amazons, including our *P. rufescens*; I have never seen but one of these ants alive—a scout taken in Boston park. *P. lucidus* is of a uniform and beautiful shiny yellowish-red colour. Wheeler, who has studied it in detail, says that its colonies are small. They often contain ergatogynes, which, as in the case of *P. rufescens*, may replace the ♀.

On July 31st, 1904, Wheeler saw about 200 *P. lucidus* come out of their nest at 2-37 p.m. and arrive at 2-45 near a crater of *N. incerta*, situated fifteen metres away from their nest. The *lucidus* poured through the opening, slaughtering or frightening away the *incerta* that were loitering about the galleries. A moment later, the first *lucidus* emerged with a cocoon, and all the rest followed, most of them being laden. One of them, which had picked up a young *incerta*, killed her on the crater. At 3-13 the last stolen cocoon was brought out of the nest. A few *incerta* which tried to defend themselves were at once dispatched by the *P. lucidus*.

Wheeler isolated thirty *P. lucidus* which had *N. nitidiventris* slaves, and watched them as they suffered themselves to starve to death in front of a dish of honey and a wet sponge. They begged one another in vain for regurgitation, and finally began to die of hunger. When only sixteen of them survived, Wheeler placed near them three *S. subsericea* ☿ and the same number of *N. nitidiventris* from strange colonies. The *P. lucidus* were more spiteful towards the *S. subsericea*, all of which they pierced and killed. On the other hand, at first they seized the *nitidiventris* by the legs

only. But when Wheeler returned at 9 p.m., he found two *nitidiventris* ☿ dead and the third in alliance with the *P. lucidus*, which she was feeding in succession with honey. All next day she continued to feed them like a solicitous mother. Nevertheless, on the day after that Wheeler found the poor, benevolent *nitidiventris* with her head pierced by one of these stupid and ungrateful *P. lucidus*.

At 3 p.m. Wheeler placed twenty big *S. subsericea* ☿, with their brood, near the sixteen *P. lucidus*. To his great surprise, it was the *subsericea* this time that attacked the *Polyergus* in the apparatus, mauled them about, caught hold of their legs and showered them with formic acid, leaving them in a pitiable plight. This victory for the *subsericea* is almost incredible, but as it is described by such a judicious and conscientious author as Wheeler, we cannot feel any doubt about it.

It follows from these facts that each of the three American species of *Polyergus* known, has somewhat different specialized habits. There is nothing either new or rare in the combination of beauty and stupidity; it can be seen in *P. lucidus*, which proves to be the fiercest of all, and without reason, when attacking the weak and cowardly *Neoformica*.

4. POLYERGUS SAMURAI. This beautiful *Polyergus*, which is quite black, lives in Japan, whence a specimen has been sent me by Prof. Tocutaro Ito. Its ♂, which is also black, has pure white legs and antennæ, which give it an unusual appearance. *P. samurai* enslaves a Japanese variety of *Serviformica fusca*; but I do not know any details concerning its expeditions. It is at least as large as *P. rufescens*.

3 *HARPAGOXENUS*

This genus consists of two species of *Myrmicinæ*, whereas *Raptiformica* and *Polyergus* belong to the *Formicinæ*. One of

these, *H. sublevis*, lives in the north of Europe, and the other, *H. americanus*, at Washington, New York State, and in Pennsylvania. These ants enslave *Leptothorax*, and constitute a kind of transition between the facultative independence of *Raptiformica* and the obligatory slave-making tendencies of *Polyergus*. But it is something apart from either of these. For the best studies of these curious ants we are indebted to Gottfried Adlerz, H. Viehmeyer and W. M. Wheeler.

1 H. SUBLEVIS. This species has been found in Finland, Sweden, Denmark, the Dresden district of Saxony, and last of all, as discovered by Emmelius in 1914, in the Swiss Engadine, at a height of some 1,600-1,700 metres. It was depicted in fig. 73. Its slaves are *Leptothorax acervorum* and *muscorum*, and occasionally *L. tuberum*. It has triangular mandibles, but they have lost their teeth. Meinert had already found five ☿ with ocelli to one without them. All possible forms are actually present intermediate between the worker and ergatogyne, which in this case is the principal sex, and, according to Adlerz, mates with the ♂ of other formicaries. This ergatogyne has a receptacle for semen, and founds colonies by attacking *L. acervorum* or *muscorum* nests alone or with the aid of companions. She drives out all the inhabitants and annexes their nymphs of all sexes, which she rears as her slaves. She often cuts off the wings of virgin *Leptothorax* ♀ as soon as they are hatched, in order to make them slaves also, for the *Leptothorax* ♀ work among the rest. She also frequently cuts off the wings of the ♂, possibly in order to make them her husbands. However, Viehmeyer has discovered in Saxony a few rare winged *H. sublevis* ♀, which have never been found in the north before.

Adlerz isolated some *H. sublevis* with their larvæ, which

they allowed to starve or shrivel up completely. For their own part, however, they were able to eat the food that was given them and accordingly to live for 135 days, but unable to go out of their nests alone in search of food. The interesting point about this is that the ergatogyne accumulates and combines the rôles of mother-queen and marauder-worker. The ♀ of *Raptiformica* does likewise, but only in the early stages of her life.

In Sweden, Adlerz found an *H. sublevis* formicary containing *L. acervorum* and *L. muscorum* slaves at the same time. Hence he deduced that this slave-making ant must sometimes raid natural colonies, as *Polyergus* does, and not content itself with the brood reared by the ergatogyne-founder. But these expeditions, and the return homewards, have never been observed. Wheeler, who found a natural mixed colony in America, consisting of the yellow *Leptothorax curvispinosus* and the black *L. longispinosus*, was induced to wonder whether Adlerz's *H. sublevis* ergatogyne in Sweden might not have attacked a similar mixed formicary of *L. acervorum* and *muscorum*, but this does not seem to me very probable; it would be an exception superimposed upon an exception. For my part, I think that Adlerz is in the right. It is nearly always the *Leptothorax* ☿ slaves which transport the *H. sublevis* and brood during removals.

Viehmeyer noticed that the slaves of *H. sublevis* feed larvæ in two ways, firstly by regurgitation and then by giving them pieces of insects which they have cut up, as the *Ponerinæ* do. This same author thinks that the slave-making instincts of *Harpagoxenus* are derived by phylogenesis from former lestobiosis. This is possible, but, I repeat, beware of hypotheses.

2 H. AMERICANUS. This extremely rare species lives with *Leptothorax curvispinosus*. Wheeler is the only person

who has observed its habits; he observed three formicaries, one containing a single ☿, another six ☿, and a third eight ☿, and a true fertilized ♀ with traces of wings and not ergatoid. There were no fertile *Leptothorax* ♀. When confined in an artificial nest, *H. americanus* proved to be completely inactive. To Wheeler these ants convey the impression of having reached a more abject stage of parasitism than their European congener, *H. sublevis*. But Wheeler did not discover how their colonies were formed.

In brief, a great deal of observation upon *Harpagoxenus* has still to be made, and various experiments, on the lines of those made by Kutter, which we shall shortly describe, have still to be carried out.

4 THE SLAVE-MAKING *STRONGYLOGNATHUS*

In 1871 the only species of this genus known as yet was *Strongylognathus testaceus*, a parasitic species represented in fig. 104, whose habits I have described in Chapter VII of Part III. The slave-making species are not represented, but they have exactly the same kind of mandibles as *S. testaceus*, and differ from them only in the shape of their occiput, which is convex and without a hollow on the posterior edge.

1 STR. HUBERI. In July, 1871, I explored southern Helvetia in order to be able to write about the ants found in every part of Switzerland. While visiting Fully in Valais, I dug my chisel into a nest of small *Tetramorium cæspitum*, and was surprised to find these ants mixed with others redder in colour, somewhat longer, and almost as numerous as themselves. I took my magnifying glass, and what was my surprise and joy to find at the first glance that I had come upon a new species of *Strongylognathus*, differing from *testaceus* at any rate in its occiput, its larger size, and the

great number of ☿ in the formicary. For the time being I named it *Huberi*, in memory of my revered Pierre Huber, and I soon made the following experiment:

I went to a place near by and filled a bag with small *T. cæspitum*, similar to those of the *S. Huberi* but belonging to an ordinary natural, unmixed formicary, and these, with their brood, I placed a few centimetres away from the *Huberi* nest. The attack with my chisel had already brought the *S. Huberi* out of the nest, and, feeling at once that the *Tetramorium* were strangers, they and their slaves formed an army and fell upon them by common accord. I saw them grasp the *T. cæspitum* by the body or head, in the manner of *Polyergus*, overwhelm them singly by their mass formation and the rapidity of their march, and finally steal the nymphs and carry them back to their nest. It was certainly they, not their slaves, that achieved this rapid victory—a fact which I cannot understand. There are, nevertheless, a few difficulties about this experiment: the foray was artificial; a relatively large number of *S. Huberi* were killed; and finally, thanks to their strategy and dash, they were quite successful in routing the *T. cæspitum*, though not in piercing their brains, owing to the hardness of the *Tetramorium* chitin.

Since that time I have found this species at Fully on two or three occasions. In 1900 I brought a whole nest back to Chigny on my bicycle, and there I established it and used it to repeat and confirm my former experiment, rearing both ♀ and ♂ meantime: but I did not manage to find the queen. On every artificial expedition against the *Tetramorium*, which I brought thither with their brood, the *S. Huberi* attacked and vanquished the *T. cæspitum*. They also stole the nymphs, but I further observed that some of these, at any rate, were afterwards rejected by the slaves—

possibly because they belonged to a slightly larger variety. In short, I began to suspect that the *S. Huberi* had already been tainted with the parasitism of the mother-queen.

At a later date Escherich, following my directions, found the *S. Huberi* nest again at Fully, and showed it to Wasmann, who, so he told me, recognized two different varieties of *T. cæspitum* in this mixed formicary. From this he concluded that *S. Huberi* makes natural raids. Since then, various races and varieties of *S. Huberi* have been discovered, among others the *S. afer* which I myself gathered in Algeria. It is smaller than *Huberi s. str.*, but the formicary contains the same number of ☿. For the most part, the varieties of *T. cæspitum* found in that district are very small.

2 S. REHBINDERI. The geologist Rehbinder once sent me some ants which he had taken on the shores of the Black Sea, near the convent of New Athos. Amongst them were ☿ of a new red *Strongylognathus*, the largest of all the species, with a much bigger head and more robust build than *Huberi*, and also an abundance of *T. cæspitum* nymphs, but no adult ☿. This aroused my suspicions, and I wrote to Mr. Rehbinder explaining the matter (the other ants were black or grey), and asking where and how he had found this new and very interesting red ant. He answered clearly and concisely by return of post, that he had taken a number of these ants, the only red species, while they were carrying small white nymphs, in broad daylight, on a gravel path connected with the New Athos convent. No doubt was possible. These *Strongylognathus*, which I baptized *Rehbinderi*, had been on a natufal expedition and were returning after plundering the nymphs of a *Tetramorium* formicary. This shows you, my dear reader, that a good observer like M. Rehbinder, even if he does not understand for the time

being the value of his observation, may afterwards be enlightened by a specialist on the matter, and, conjointly with him, succeed in solving an important problem. The thing that really matters is good observation; Mr. Rehbinder had no idea that this was a slave-making expedition, but he had seen clearly and accurately—and that is the basis of all scientific induction. A fig for hypotheses! I for my part was sufficiently well acquainted with *Strongylognathus* and the *T. cæspitum* nymphs to avoid any mistake; for the rest, the ☿ are still in my collection.

There are, then, species of *Strongylognathus* which carry out spontaneous forays. But further proofs of this are to follow.

3 S. HUBERI ALPINUS. This Alpine race, discovered in 1909 by Wheeler at Zermatt in Valais, nearly 1,800 metres above sea-level, is quite distinguishable from other *S. Huberi* by its more robust (less slender) stature and darker colour. Wheeler found several formicaries of his new race containing one *alpinus* to 3-5 *cæspitum*. Once he found sixty *alpinus* and only two *T. cæspitum* under a stone. He discovered the ☿, ♂ and ♀ nymphs of *alpinus*, but only the ☿ nymphs of *Tetramorium*. He repeated in front of a large formicary the experiment which I had made with *S. Huberi*. In a quarter of an hour's time the *alpinus* came out in crowds, seized the *Tetramorium* by their heads and bodies and then carried away the nymphs, which were not rejected by the *cæspitum* slaves.

Wheeler rightly declares that no formicary so enormous as those he found can be explained by the rape of nymphs. He supposes that raids take place at night, and that, under certain circumstances, the marauding army retires beneath the stones in the day-time, owing to its fear of heat, as in the above-quoted case of the sixty *alpinus*.

But, for the most systematic and complete experiments with this extremely interesting ant, we are indebted to Heinrich Kutter, of Zurich. He begins with the following summary of the observations which he made upon natural nests before 1920:

I All the south-eastern slope of the valley, 1,600-2,050 metres in height, is populated by *S. alpinus*.

II Their formicaries vary in size from small nests to large polycalic states.

III The proportion of *alpinus* to the *T. cæspitum* varies from 1-1 to 1-15 or 1-20; on an average it is 1-4 or 1-5.

IV One nest found by Wheeler had no brood but that of *alpinus*.

V On three occasions a large number of *alpinus* were found with very few *T. cæspitum*.

VI Only one out of five experiments testing the slave-making instinct in *alpinus* showed any reaction, and then not until a quarter of an hour had elapsed.

VII The brood of strange *Tetramorium* were always eagerly accepted by the slaves of *alpinus*.

VIII Hitherto no fertilized ♀, ♂ or ☿ of *T. cæspitum* have been found in a *S. alpinus* colony.

IX No natural expedition of *S. alpinus* has so far been observed.

X The nuptial flight of *S. alpinus* takes place at the same time as that of *T. cæspitum*.

As he was not successful at Zermatt, Kutter took a bag full of *alpinus* and their slaves and brought it to Zurich, where he placed them in an artificial nest (Meldahl-Kutter system) in communication with the large framed arena which we described in Chapter I of Part III. We will use the letters T.S. to denote the nest of the mixed *Tetramorium* —*S. alpinus* formicary, which contained between 140 and

200 ☿, 100 winged ♀, a few ♂ and some *alpinus* young-besides some 600-800 *T. cæspitum* ☿.

On September 3rd, when everything had settled down, the nuptial flights took place; the sites of the cemetery and manger were fixed. On September 8th Kutter went to a natural formicary and took 400 *T. cæspitum* with their abundant ☿ nymphs, all of which he placed in an artificial apparatus identical with that of the T.S., but situated at the other end of the large arena. This may be called T.N. In this manner the two formicaries were able to come in contact with each other as though accidentally and naturally.

Kutter soon saw a few *Tetramorium* from the two formicaries grappling with each other in the arena. But besides this, more especially towards the evening, several *Strongylognathus* (which we will call S.S.) approached the T.N. nest, and one of these spies was even attacked by a T.N. and defended itself with its mandibles. A few T.S. and S.S. ☿ went so far as to enter the T.N. nest, but they were ill received and fled back to the arena. The T.N. then obstructed the entrance to their nest, as far as a narrow passage, with small grains of sands, and the few T.S. which had not saved themselves in time were killed.

In the meantime, evening had fallen. By the light of an electric lamp Kutter then saw the S.S. growing excited and following one another in close files out of their nest and along the left edge of the arena. But when they had gone a third of the length of the arena, on the side opposite to that of the T.N. nest, the file retraced its steps and continued thus returning upon itself unceasingly. The presence of the electric light on the left may have caused the S.S. ☿ to take the wrong direction. Doubtless they felt bitter towards the T.N. But it was late at night, and Kutter was obliged to retire.

At 6-30 a.m. on the following day, September 9th, the slave-making expedition was in full swing. And a curious expedition it was! On raising the cardboard cover of the T.N. apparatus and letting the light into the interior, Kutter saw some 50-60 S.S. All the grains of sand heaped up the previous day by the T.N. had been cleared away. The T.N. were huddled together, motionless, either on their brood or at the sides of their nest; the temperature was fairly low, and this made them lazy and totally indifferent to the S.S., which seemed to have intimidated them completely and were behaving like the masters of the T.N. house. Several *Tetramorium* couples were also seen fighting each other. A few T.S. must, therefore, have found their way into the T.N. nest. Indeed, though the S.S. coming to and fro between the T.S. and T.N. nests, this time on the right side of the arena, were at very wide intervals, Kutter saw in their midst a few T.S. The *Strongylognathus* were zealously carrying the T.N. larvæ and nymphs into their T.S. nest without being molested by the T.N. Sometimes they would be tripped up, but, unlike the ants in Kutter's natural formicaries at Zermatt, they were never seen to relinquish their booty for this reason. On the road that lay between the two nests in the arena, he saw as many S.S. returning to the T.N. nests without spoil as with it. They all followed the vertical edge of the arena which formed a right angle. None of them crossed straight over the arena between the T.S. and the T.N.

The fighting tactics of the *alpinus* S.S. were extremely comical. They prudently grasped hold of their enemies from behind, preferably by the thorax. Without doing them any serious harm, they obtained mastery over them by a notable tactic. The *T. cæspitum* seized in this way would fold up its legs and the abdomens of the two ants

would begin to tremble violently, especially that of the *Tetramorium*. The *alpinus* soon relaxed her hold and went away, as though overcome with disgust for the T.N., and also as though she had no other means of overawing this creature, which was at least as strong as herself. The S.S. was not fond of making a frontal attack, and if she did so, she took hold of the T.N. by the neck, pronotum or mouth, and raised herself up. When she was free again, the T.N. seemed half frightened and half subdued; her fighting spirit had disappeared. Probably the low temperature had its share in the production of this phenomenon.

Thus it happened that the keen and lively *alpinus* managed to walk about with impunity amid the crowd of T.N. Sometimes, however, a T.S. became excited and ran away, though Kutter never saw it attacked by a T.N. in such a case. It was always the S.S. which fooled the T.N. in the manner described above. The T.N. crouched in a motionless heap over their brood. Kutter thought that the S.S. would find it difficult to steal their brood. But not at all! Our S.S. gripped one T.N. after another by the back and carried her out of the way until the brood was revealed and the nymphs could be removed. But over and above this, the S.S. tried to pester the motionless heap of T.N.; they carried little stones among the *T. cæspitum* ☿, as though they wished to bury or excavate them, certainly for the sake of annoying them. At 10 o'clock in the morning a great deal of the brood still remained, but there were only five S.S. left in the T.N. nest. When a S.S. was caught by a T.N., she feigned death and hence quickly obtained her freedom; this was observed several times by Kutter.

Altogether the *S. alpinus* seem to have a talisman (which is perhaps only their strategy) that enables them to go into all sorts of places whither their slaves can penetrate only

after fierce fighting. In any case, the 'masters' were much less dangerous to the T.N. than their T.S. slaves, which accompanied them and waged relentless war on them throughout the day. For several days the T.N. nest was visited in this way, and its population continued to diminish. During the night and until the following morning the S.S. kept running out and carrying off the nymphs. At 2 p.m. on November 9th, for instance, there were only two S.S. in the T.N. nest, but at 7 o'clock in the evening there were twenty-five again. This evening the to-and-fro movement along the left side of the arena was still more marked. One or two *alpinus* ♀ twice visited the T.N. nest and fought with the T.N. in the same manner as their S.S. ☿.

Kutter vouches for the fact that the T.S. adopted the nymphs of the T.N. Two larvæ only were thrown away into the arena. Towards the end the S.S. gave up transporting the young from the T.N. nest to the T.S. nest, and the T.S. ☿ alone discharged this duty. The *S. alpinus* carried the T.N. ☿ peaceably to their nest. Finally a few S.S. ☿ discovered the direct route between the T.S. nest and the T.N. nest.

By the evening of September 14th the T.N. nest was completely emptied of ants and brood. Kutter then counted about 100 dead among the *T. cæspitum*, and only one ☿ and one ♀ dead among the S.S. He is convinced that the *T. cæspitum* (T.S.) alone had nearly all these murders on their consciences. As early as November 13th he ascertained that the number of *T. cæspitum* in the T.S. nest had increased. "Behold how a robbers' foray was transformed into a union of peoples." Such is Kutter's description. Would that it might be likewise with our poor human race at the present day, despite the blindness of those who govern it! Kutter summarizes his results as follows:

I *S. alpinus* is liable to make spontaneous slave-raids.

II Apparently these raids can take place only at night. The above experiments in the arena confirm observations made under natural conditions. This would seem to be an adaptation: at Zermatt a fierce sun strikes vertically, from morning till evening, upon the bare slope occupied by *S. alpinus*, and the ants dare not go out until the evening, when the rays have been intercepted by Mont Cervin.

III Some of the slaves may accompany their 'masters' on the forays. The three bands of *S. alpinus* found under the stones by Wheeler and Kutter, and containing a very small number of *T. cæspitum*, were doubtless raiding-parties delayed by the sun. This supposition is confirmed by the experiments made in the arena.

IV The raids of *alpinus* have quite a different character, however, from those of *Polyergus*, and probably from those of *S. Rehbinderi*. They form up in narrow, unbroken files which tend to connect the mixed slave-owing formicary with the natural formicary invaded by the *T. cæspitum*.

V During these raids the *S. alpinus* prove to be less formidable to the *T. cæspitum*, individually speaking, than their slaves. Consequently, the *S. alpinus* allow their slaves to fight, and concern themselves only with intimidation and the rape of the nymphs, though towards the end they leave this last task to their slaves.

VI All the experiments, which Kutter repeated several times, ended in an alliance between the robbers and the robbed, and all that were left of the defeated ants were finally removed to the mixed formicary and annexed by it.

VII Alliances of this kind are facilitated by the nocturnal pillaging expeditions of *S. alpinus*, which occur when the fall in the temperature makes the *Tetramorium* lazy, sleepy and much less combative than they are by day.

VIII The curious fighting-method of *S. alpinus*, consisting solely of intimidation, also facilitates their final alliance with the *T. cæspitum* which they defeat.

IX According to Kutter's experiments, the *S. alpinus* ☿ and even its ♀ are capable of digging nests for themselves and eating without any assistance.

X In the mixed formicaries, Kutter has been unable so far to discover any ♀ undoubtedly fertilized, among either the *T. cæspitum* or the *S. alpinus*, though he certainly found some *alpinus* ♀ which had lost their wings.

XI It is probable that *S. alpinus* also carries out underground raids. Its formicaries are sometimes enormous, and may occupy more than five square metres.

XII Kutter once put seventy *S. alpinus* with seventy very lively *T. cæspitum* and their brood. At first the *alpinus* seemed as though they were defeated and overwhelmed, and allowed themselves to be maltreated by the *Tetramorium*, which were apparently frantic with rage. But by slow degrees the *alpinus* began to defend themselves and to take hold of their furious enemies by the head and thorax. In the end Kutter counted twenty dead *alpinus* and sixty-one dead *T. cæspitum*. On being released after hand-to-hand encounters with the *alpinus*—so Kutter wrote to me—the *Tetramorium* often seem to be stupefied and afflicted with paralysis in their mandibles and front legs. This may be the result of wounds in the neck or brain, which the hooked jaws of *S. alpinus* reach through the mouth, as Kutter has frequently observed. He thinks that the sub-oesophageal ganglion has been broken in front of the prosternum or through the mouth.

Such are the admirable observations and experiments of my young friend Heinrich Kutter, published in the *Biologisches Zentralblatt*, Vol 40, 1920. From these, dear reader, you

should derive yet another warning against generalizations. Every species or race of *Strongylognathus* seems to have special habits; *S. testaceus* has become a parasite and no longer goes raiding, but its ancestors must have done so, as it betrays phylogenetic reminiscences of the slave-making instinct when placed in the presence of strange *T. cæspitum*. *S. Rehbinderi* goes on raids by day in the open air, but nothing more is known about this species. *S. alpinus* seems to be peaceably disposed, but it goes on nocturnal raids, probably sometimes under ground, which are faintly suggestive of the expeditions of *Raptiformica sanguinea* in the uninterrupted character of the files between their nest and the plundered formicary, though quite different in other respects. As yet we know of no spontaneous raids on the part of *S. Huberi*, and its artificial expeditions seem to resemble those of *alpinus*, except that they exact rather more energy. Until more evidence is forthcoming we cannot tell whether they are conducted by day or night. In any case, I think I must now withdraw my accusation concerning its tendency to parasitism as an unjustifiable suspicion, from which its cousin *alpinus* has cleared it. We know nothing yet of the other species, *afer*, *Christophi* and *Cæciliæ*.

Kutter has also been good enough to place at my disposal a summary of his very striking experiments with a formicary of *S. alpinus* transported from Zermatt to Zurich and observed by him between 1920 and 1922. I offer the following free translation of his observations and I must beg the reader not to forget that 'I' refers here to Kutter, not to myself.

5 THE STORY OF A CAPTIVE FORMICARY OF *STRONGYLOGNATHUS HUBERI* R. *ALPINUS*

"At Zermatt in August, 1920, I discovered a flourishing

tribe of *S. alpinus*. It was so large that when I brought it with me to Zurich I needed three artificial nests in which to accommodate it, along with its plentiful brood and its countless winged ♂ and ♀. But even these were not enough. In order to provide these creatures with the space and the number of canals essential to the way of living they prefer, I was obliged to lay out long but minute passages of glass, covered with sand, in my large arena (see above and Part III, Chapter I—Forel); these passages branched out and led directly to the entrance and exit-passages of the three nests. As soon as everything was ready the ants ran out into the arena and spread into the branching tubes. Two hours later, at 1 p.m., the winged ♂ and ♀ of *S. alpinus* emerged in a state of great excitement and set out on their nuptial flight. But while the ♂ flew alone as far as my window, which was facing the sun, the much heavier and more lethargic ♀ were scarcely able to sustain their flight till they were outside the walls of the arena. During the days that followed the same facts were repeated and still further accentuated, as I observed several times. The ♂ could scarcely be restrained long in their native nest, whereas the ♀ often remained there without even making serious attempt at a nuptial flight.

My colony was soon quite at its ease in its new abode; I could see that this was so by the hardworking and well-regulated life it led.

Set apart in a fourth artificial apparatus, I had a fine colony of pure *Tetramorium cæspitum*, taken at Zermatt, which contained some hundreds of nymphs and also the winged forms of both sexes. On September 10th, at 5 o'clock, I put this nest into communication with the arena, in such a manner that on coming out its inhabitants would inevitably enter into direct communication with the tubes

of glass under the sand belonging to the *S. alpinus* establishment. As I expected, the two formicaries soon came in contact with each other. But, to my great astonishment, the intensely warlike *S. alpinus* then remained still, showing no sign of hostility or any kind of reaction. Only a few isolated combats between *Tetramorium* betrayed the fact that two strange formicaries had come unawares into each other's presence. The *T. cæspitum* went quite peaceably in and out. In four hours' time (about 9 o'clock) I even saw a few *S. alpinus* walking calmly into the nest of the pure *Tetramorium* without being attacked.

It may be suggested that the two formicaries had perhaps already been allied with each other at Zermatt. We can scarcely assume this, as their nests there were situated at least 200 metres apart and separated furthermore by rocks, goat-sheds, heaps of manure and countless stones and slopes, such as are found everywhere in the Alps. The explanation must be sought elsewhere, namely, in the temporary situation of the two groups, which compelled them to make a peaceful alliance when they suddenly met by artificial arrangement. The *S. alpinus* were absorbed in their nuptial flight; the strange *Tetramorium*, overtaken unawares, had to provide for an enormous brood, as the slaves of *S. alpinus* were also obliged to do. Hence they had no time for fighting. Anxiety for the brood and the nuptial flight must inevitably have led the two parties to an alliance.

The new and free *Tetramorium* formicary soon began to transport its brood into the forked canals (of the arena). The heap of brood in the three *S. alpinus* nests increased to such an extent that it had also to be carried into the same canals beneath the sand. These canals seemed to be specially pleasing to the ants. Very few *S. alpinus* took any individual share in the transport of the nymphs; hence this can hardly

be described as a slave-raid. On the other hand, a few *T. cæspitum* struggled to reverse the process, and re-transport nymphs from the canals to the nests; but they were overpowered. Altogether, therefore, this affair may be called a peaceful alliance, disturbed only in its early stages by a few isolated individuals.

But the most interesting point is still to come: never a day passed but the *Tetramorium* ☿ (naturally I could not discern whether they were the former slaves of *S. alpinus*, or their new allies, or both), would set to work pursuing and plaguing the winged ♀ and ♂ of their own species, and at last cutting off their heads until all had perished miserably. On September 1st I gave them seven more ♀ and two more ♂ which I had kept apart, and they endured the same fate.

My first experiment ended, therefore, in an almost undisputed alliance, and the murder of the *Tetramorium* winged sexes by their own ☿. I was even surprised at first to see how eagerly the *T. cæspitum* ☿ of the two formicaries licked each other, instead of fighting. The *S. alpinus* played an almost passive rôle. True, these slave-makers helped a little in the transport of the nymphs—not without occasional friction—but that was all. Their ♀ and ♂ kept swarming all day long, and this apparently distracted the attention of the ☿ from war; they were seen among their winged brothers and sisters, but very seldom among the strange *Tetramorium*.

I had several more opportunities of seeing the *Tetramorium* murder their own winged sexes, but I also saw many cases in which they were kind to them; everything depended on the circumstances, which varied. The points deserving of emphasis are: 1 that the murders in question have been proved many times over; 2 that the *S. alpinus* never took any part in them.

I afterwards repeated this experiment with a weaker colony of *T. cæspitum* from Zurich, containing 250-300 ☿ and 80-120 nymphs. This time, however, I made the exit-tube of their artificial nest 2½ metres longer, so that any slave-raid made by the *S. alpinus* would have been obliged to pass from the arena to a table on which I had placed the new *Tetramorium*.

But once again my *S. alpinus* played me false and showed no sort of inclination to try the adventure. The nuptials of their winged sexes did come to an end, and the nest was overfull of an almost adult brood. From a human standpoint it is easy to understand their behaviour, but it would be rash at this stage to assume causes of this sort. *Tetramorium* slaves, on the other hand, soon found occasion for vindictive quarrels with the newcomers. They found a way into their long tubes, and I saw some couples fighting savagely with each other and curling up their abdomens. The *T.* slaves arrived at the enemy nest, whose defenders had barricaded it with earth, and exterminated them one by one with the consistent tenacity peculiar to *T. cæspitum*. A few scattered *S. alpinus* also arrived and even carried off a few nymphs, but this was not enough to constitute a slave-raid.

My *S. alpinus* formicary was evidently not to be urged into any more raids during the rest of the year 1920. Towards the winter, the ants withdrew more and more to their nests; in the end they even concentrated into one nest, so that I was able to close the two others. Meanwhile all the *S. alpinus* ♂ and ♀ had flown away or were dead. In January, 1921, no more ants were found in the arena, and accordingly I was able to close the arena-doors as well and leave the ants in their apparatus until the following spring.

It was in March, 1921, that the first *S. alpinus* wakened.

a. *Camponotus* (*Mrymosericus*) *chilensis* v. *ruficornis* ☿. Chili. 10 mm.

b. *Polyrhachis* (*Chariomyrma*) *Hookeri* ☿. Australia. 4·5 mm.

c. *Polyrhachis* (*Hedomyrma*) *ornata* ☿. Australia. 6·5 mm.

d. *Polyrhachis* (*Chariomyrma*) *caulomma* ☿. New Guinea. 8·5 mm.

d. Polystemon (Cytinaceæ) columnæ ♀. New Caledon. 8.2 mm.

c. Polystemon (Hydnoraceæ) ovarii ♀. Arabia. 9.2 mm.

β. Polystemon (Cytinaceæ) Hookeri ♀. Australia. 4.2 mm.

α. Cytinus (Ustilaginaceæ) ovarium ♀. Capit. 10 mm.

In winter they had never been seen outside the nest—not even in the manger, but henceforth they could be seen there in great abundance. During the spring and the beginning of summer I united my formicary with two other small groups of *S. alpinus*, also from Zermatt, which I had kept separate. I may mention, in passing, that their story would be no less interesting than that given above. On June 26th I again placed the arena in communication with the formicary, in the hope that the performances of my little circus of ants would begin again. More and more *alpinus* ☿ came into the arena, while their slaves naturally ferreted about in the manger for food, cleaning it meanwhile.

During the whole of the preceding year at Zurich, therefore, my *S. alpinus* had abjured their violent nature. In all my experiments quoted above, the *Tetramorium* slaves had played a predominant rôle. I was anxious this time to eliminate their influence artificially, by simulating the natural state of affairs—at any rate, to limit it as far as possible. With this end in view, I simply starved my formicary.

On August 18th I took, near Zurich, a thriving formicary of *T. cæspitum*, consisting of large, strong ☿, much stronger than the small, thin ☿ from Zermatt. This lot consisted of some 1,400-1,600 ☿ and 900-1,100 larvæ and nymphs. Between the exit tubes of the two nests I scattered some sunflower-seeds and drops of honey to attract the famished slaves of the *T. cæspitum*. We will call the newly arrived *Tetramorium* T.N. (as above—Forel), and the slaves of the old mixed colony T.S. First of all, the T.N., which were coming out in a crowd, and the T.S., which had fallen upon the victuals, met each other. The large Zurich ants were twice or thrice as many as the little T.S. Their numbers and

their abundant brood, moreover, increased the natural combativeness of their spirit, as the first battles proved. The superiority of the T.N. seemed to be assured, and it was with some trepidation that I watched the decisive battle which was steadily developing.

Scarcely half an hour after the beginning of the experiment a somewhat widely-scattered band of about fifty *S. alpinus* approached the entrance to the T.N. nest. The slaves, after their long fast, were so much absorbed in the attractions of the victuals that the action of their masters was all the more distinctive.

The few *S. alpinus* at once tried to find their way into the T.N. nest, but as soon as they were in the arena, not to mention the entrance-tube and the nest itself, they were attacked so violently that I thought they were doomed. Soon, indeed, I saw that each of them had four or five big T.N. tugging at her limbs and maltreating her atrociously. I had watched many a *S. alpinus* expedition, but never before had I seen them faced with such a strong and courageous foe. I therefore observed the fight like a doubting Thomas, but those artful rogues the *Strongylognathus* soon found a way of demonstrating their occult power. Within two hours they had won a decisive victory. Their fighting ardour was fairly moderate at first, but it grew every moment. They obtained reinforcements, but even so they were compelled to hold their own against an enemy which, apart from size, was at least ten times superior to them in numbers. Yet they were soon the absolute masters of the situation. Once the T.N. were disheartened their only thought was to flee altogether to the bottom of the nest and hide their brood; but here also they were pursued.

All the scenes that followed were identical with those of other *S. alpinus* raids. Crowding in every direction, these

ants set to work consistently to torment the T.N. in their importunate manner (see above—Forel), while the large *Tetramorium* had exchanged their initial fighting fury, and even their activity in saving their brood, for a completely phlegmatic state of resignation. In direct contrast to the customary ways of the *Tetramorium*, the *S. alpinus* showed once more their scorn of the enemy's obstinate attempts to bite them in hand-to-hand contests. Moreover, the large number of dead or paralysed T.N. proved to me what terrible enemies these *S. alpinus* were to that species. In the evening they were seized with a veritable lust for plunder. The ☿ dashed from one nest to the other as though vying with one another in bearing the nymphs and larvæ away. Thus the entrance to the T.S. nest was soon blocked and its chambers were filled with the stolen brood; yet the *S. alpinus* did not cease their rapine. At first some of the slaves were not agreed among themselves, for I saw several T.S. bring out nymphs and throw them into the arena (compare with *Strongylognathus Huberi* above, under 4, No. 1—Forel): but they could not possibly counterbalance the *S. alpinus*' zeal for accumulation. Morever, some other T.S. ☿ began to pick up the nymphs rejected by their companions, and also to pay personal visits to the nests of the hopelessly defeated T.N. and steal their brood.

On the morning of the following day, August 19th, the *S. alpinus* were still in the full flush of their activity. But as there were scarcely any more young to carry off the gay fellows turned their attention to big T.N. themselves, much to their disapproval. By pinching and biting, and causing them all sorts of annoyance, the *S. alpinus* forced them to coil up and allow themselves to be borne away to the nest and adopted. This was a veritable slave-hunt in the strictest sense of the word—much stricter than in its

application to the *Polyergus*. In this case the rape of the brood was not enough; the adults were likewise compelled to knuckle under and become abject slaves.

In this way the fine strong T.N. formicary was entirely destroyed, its brood was stolen and most of the ☿ were carried away and to some extent pursued and pestered by the *alpinus* ☿; it seems as though these creatures wished to give them a lesson in docility. In the plundered nest, the *S. alpinus* behaved like the sole master of the abode; the few remaining T.N. hid themselves in every corner, but they could not escape the general fate. About August 21st, indeed, some two or three hundred of them gathered together under their apparatus, which stood in the arena, and there tried to hide and save between fifty and a hundred nymphs; but the *S. alpinus* discovered this hiding place too, and once more removed its contents. Yet more bickering took place between the T.S. and T.N., but now they were never violent; for that matter, utterly intimidated as they were, and confused as to their bearings, the T.N. would not have been capable of violence. On the following day I was able to close their nest and remove it from the arena.

Another *Tetramorium* formicary which I sacrificed a week after to my *S. alpinus*' lust for plunder endured the same fate as the T.N. Exactly the same phases followed one another: a furious attack by the new *T. cæspitum* to begin with, ending in bodily capture and slavery for them.

My *S. alpinus* formicary was only able partially to endure the second winter, 1921-22. By the spring of 1922, indeed, the *S. alpinus* had practically disappeared. The T.S. had still a large number of larvæ, but they no longer showed any inclination to take up their abode in the arena and remained quietly in their nest. Some *Formica fusca* ☿ which I had

placed in the arena discovered the entry to their nest and killed as many T.S. as they could in order to take their place. The only refuges in which the T.S. managed to subsist a few months longer before disappearing were a few hidden chambers whose entrances were too small for the big *F. fusca*. Thus ended the Iliad of my *S. alpinus*."

I must certainly admit (I, Forel, now take up my pen once more) that I was far from expecting the surprises thus revealed to us by Kutter, thanks to his arena and his ingenious experiments. Here we find *Tetramorium* slaves killing their own winged sexes, and *Strongylognathus Huberi* r. *alpinus* turning out to be really a much worse slave-maker than *Polyergus*, not to mention *Raptiformica*. Surely no one would have suspected it of reducing adults to slavery—but what an error was mine when I doubted the slave-making capacities of *S. Huberi!* Truly, the scales have fallen from my eyes. There can be no doubt whatever but that the pure *S. Huberi* of Fully behaves in almost the same way as its somewhat distant cousin, the *alpinus* race of Zermatt. In any case, the partial rejection of the stolen nymphs by the slaves at Chigny in 1900 is now explained. But we have still to show how the ♀ of *S. Huberi* and *alpinus* found their new formicaries.

Here I conclude my account of the alliances, wars and slavery of ants. At the end of this work I have added an Appendix, consisting of a study which Professor E. Bugnion has kindly authorized me to publish under his name, and dealing with the observations which he made in Ceylon, on the wars of ants and termites. I would also refer the reader to Chapter IV above.

Ponder well, friend reader, the contents of the present Part, and extract from it for your own advantage a sound

and lasting gospel of peace for our unfortunate human race, still distracted by an unnatural hatred, as hypocritical as it is conscienceless, of our fellow-men of different nations and peoples. Say to yourself: "All this must cease; it is crazy beyond all endurance." We must set up a universal human system of parabiosis or alliance, to replace our antique slavery, our collective lestobiosis, our social cleptobiosis, our fraternal wars, by one well-organized and well-co-ordinated polycalic formicary extending throughout the world. Learn from the universal religion of the Persian Bahais. "Where there is a will, there is a way."—Shout this from the housetops to the League of Nations at Geneva, ere it is too late!

PART V

Part V

INTRODUCTION TO PART V

In Parts I-IV we have described the structure, classification, genesis, geography, sensations, physiology, psychology and general habits of ants, both inside and outside the nest. The task still remaining is to give some account of the special habits which are peculiar to certain more or less well defined groups in the five continents, inasmuch as we have not so far dealt exhaustively with these peculiarities.

We shall divide Part V, not including the epilogue, into seven chapters :

CH. I: The wars of the visiting ants, or *Dorylinæ*, against other living beings
CH. II: The granaries of Harvesting Ants
CH. III: The Mushroom-growing Ants
CH. IV: Weaving Ants
CH. V: Ants as janitors
CH. VI: The *Rhagomyrmicinæ*
CH. VII: Diversa
1 The *Ponerinæ*
2 The *Pseudomyrmini*
3 The *Cremastogastrini*
4 The genus *Pheidole*
5 Tree Ants
6 Ants of the Desert and the Steppes
7 Agile ants and sluggish ants
8 Jumping and projecting ants

We shall then conclude our work with an epilogue, which will be divided into four sections:

I What is a living creature?
II The rôle of ants in nature.
III Ants, termites and man.
IV What can we hope for the future of humanity?

In the first two sections we shall summarize our knowledge as to the part played by ants among the living creatures of our little planet. In the third section we shall compare them with their social peers the termites, and in the last, with human beings; for in regard to our social conditions, now in a state of flux, they will be able to yield us invaluable information.

Chapter I

WARS OF THE VISITING ANTS, OR DORYLINÆ, AGAINST OTHER LIVING BEINGS

The terrible visiting ants include three tribes; the *Dorylini*, *Ecitini* and *Leptanillini*. The first, found chiefly in Africa and to a less extent in India, is the most fearful of all. In Part III, Chapter III, sec. 9, we have described the migrations of the *Dorylini* according to Vosseler (1906). Here is a translation of this same author's account of the habits and depredations of the 'Siafu' (a Negro term), in other words, *Dorylini* of the sub-genus *Anomma*.

"Visiting ants are dominated by a spirit of perpetual unrest. No matter where the human eye encounters them, it sees nothing but headlong pursuit, fighting and slaughter. Whenever these *Anomma* appear, there are always a few which begin by running hither and thither with an excited air, feeling and probing the ground on every side. Before ever these first scouts have apparently become familiar with the surrounding district which the Siafu are preparing to invade, impatient crowds may be seen emerging from small cracks in the ground, which they hasten to enlarge. In an instant, hundreds of *Anomma* become thousands and hundreds of thousands. As though at the stroke of a magic wand, their warrior-legions rise out of the earth and spread in all directions, like a torrent without bounds, over the ground and the low-growing vegetation, which they cover

with their seething masses. Then life comes surging up on every side. Aroused as at the sound of a trumpet by the outrush of the Siafu, all living creatures, large or small, armed or defenceless, thereupon take to flight—crickets, cockroaches, spiders, millipedes, caterpillars, worms and many more, whether they are in the ground, or in decayed wood, under stones, among the grass or on bushes. All these live things, which have hitherto deemed themselves safe, flee as though demented before the implacable army, inasmuch, at any rate, as their nature allows. Thus without further ado there begins a sanguinary drama, incomparably poignant and vivid. A large bear caterpillar (moth), losing faith in its thick covering of stinging hairs, hastens away down the road, arching its back and pursued by the *Anomma* like a pack of wolves thirsting for blood. The chase is continued over a steep slope, the hunters following close upon their prey. Suddenly the caterpillar falls over, and the Siafu lose its track for an instant. Before the hapless wretch has found its feet again, however, between ten and twenty *Anomma*, or even more, have rediscovered it and bitten at its hairs, and in the twinkling of an eye some hundred ants have stopped it, swarmed over it and torn it to pieces. The fragments thus dissected are then carried away by a proportionate number of the indefatigable Siafu ☿, which bear them to their provisional nests in spite of all the difficulties of the road.

Farther ahead, a cricket is using all the strength and leaping power of its legs, with their muscles and tendons, to escape from the danger it has been prompt to recognize. Vain are its efforts! It is surrounded, seized by the legs, antennæ and wings, and then artistically dissected by dozens of sharp mandibles; its fragments go the same way as those of the caterpillar."

Here I will interrupt Vosseler's tale in order to request my readers to look at fig. 107 *C D E* which represents the ♃ and ☿ of *Anomma*. The curved mandibles of the ♃ (*C*), each of which bears in its middle a strong triangular tooth, used in clinging to the skin of a victim, would be incapable of cutting the latter to pieces. But the ☿ of various sizes, *D* and *E*, have mandibles with only a slight curve, which cross over each other when they are closed and have only two, or more often three, very oblique teeth near their extremity, so that they can bite and cut. But we must return to our observer:

"The first invaders have thus made quick work of clearing the ground. The troops which follow them up form between six and ten columns, a finger-length broad, to replace or fill up the front ranks when their predecessors return laden with booty. On every spot of ground still covered with these murderous hosts, swarming and prowling, a network of branching paths is formed, separating and joining together again, while the general movement in which the turmoil began shifts farther along the way. These paths serve both for the advance of the laggards and the return of the *Anomma* laden with prey. Soon all is well-co-ordinated, and the sides of every path are occupied by the large ♃ (*C* fig. 107), which station themselves in a serried line, shoulder to shoulder, perpendicular to the road followed by the ☿, and turn their heads outwards, waving their antennæ in every direction in search of intruders. On receiving the slightest indication that an enemy is at hand, a ♃ raises its head and prothorax in a direction perpendicular to the ground, and opens its mandibles wide, so as to be ready to seize the enemy, resting its antennæ meanwhile against these open mandibles. If, after a while, no enemy (or prey) appears, the guard

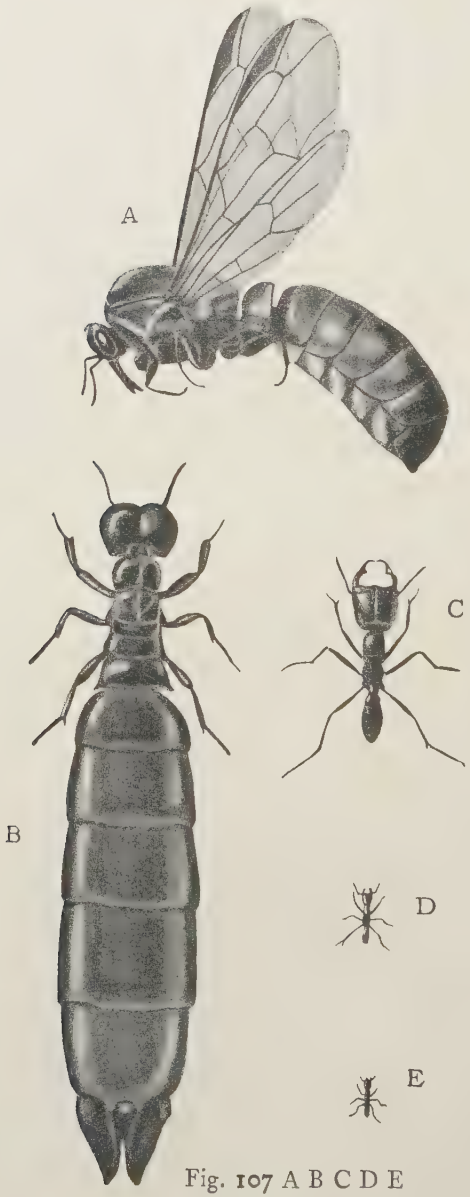


Fig. 107 A B C D E

melts away, and at last only the giant ♃ remain on the watch, with heads raised, mandibles ready to bite, and vibrating antennæ. Thus protected, the seething mass of toiling ☿ goes running on for hours and days; sometimes they all travel in the same direction, sometimes they cross each other's paths, laden frequently with fragments of prey. From time to time the current flows backwards and the guard is displaced or relieved.

When a path or network of roads has long been utilized by the *Anomma*, they build raised embankments leading to it laterally; sometimes they even cover over parts of these roads (covered paths) entirely, but there are always open intervals between two of these. Inside the embankments, the guards hang vertically, with heads bent back, so that the vertex of one almost touches that of a neighbour, and the chain of heads on either side almost forms a kind of roof to a living tunnel. Places which are often disturbed, such as paths used by men, are occupied in great strength. Swarms of ants, reaching to a distance of nearly 2 metres from the army, defend the road and its traffic against any attack or disturbance."

"The rapidity with which the Siafu mark out their roads forbids them to employ any art in their work. Even on smooth plains," says Vosseler, "these roads describe curves and meander to no purpose. On the other hand, the ants avoid stones and tree-trunks, or dig beneath them. When part of their road is flooded by torrential tropical rains the *Anomma* immediately gather together to form balls of about a hundred individuals. Thus massed, they continually change place; water makes scarcely any effect upon their smooth and oily chitin, so that the risk of drowning is reduced to a minimum. Even after floods lasting for several hours the Siafu balls remain alive and well, and as

soon as the rain ceases the ants continue their way as though nothing had happened. But as a rule, even before this, the balls are already driven by the water towards dry land. I once managed to follow, over an uninterrupted space of about 400 metres, a Siafu-road which thrice rose and fell between 40 and 50 metres. But as is often the case, I could not discover where this road ended; hence it may have been prolonged still further. According to my observations, the manner in which the *Anomma* build their nests is intimately related to the habits of these ants and explains various special points in connection with their customs.

Unlike most ants (not including *Ponerinæ* or other *Dorylinæ*: Forel), the Siafu are purely carnivorous, miniature wild beasts, of incredible voracity and fierceness, like *Eciton* of Brazil, etc. Their feeding habits compel these ants to be hunters. When they are established in provisional quarters and have occupied or built a nest, they set out from this central point to organize hunting columns in the neighbourhood, and these columns may extend for more than 100 or 200 metres. If the invaded region is rich in prey, the Siafu remain there for a fair time and complete the building of their roads. As soon as the prey in the neighbourhood is exhausted, the Siafu emigrate to another place and begin constructing more roads. Upon the success of their hunting, therefore, depends the length of time for which a road is utilized, and the degree of perfection observable in its provisional architecture. When the whole district has been well explored the *Anomma* go on a few more reconnoitring expeditions, and do not decide on a removal until their prey no longer suffices to feed them or their brood."

It is the task of the ♀ and ♃, Vosseler tells us, to initiate and carry out every new migration—to seek out

the most propitious spot and prepare for the whole process. "The *Anomma* nymphs are naked and cannot endure the sun. This is the reason why a covered road must be built upon bare ground." Here I would refer the reader to Chapter III, sec. 9, Part III, where we quoted Vosseler as to the Siafu migrations. But to continue his story:

"The Siafu work day and night, in all weathers, but to a less extent during great droughts or long rainy seasons. In their hunting they confine themselves to the ground itself and the low-growing vegetation. They rarely climb higher than a metre and a half above the earth. In human dwellings, however, they make an exception to this rule and often cover all the walls, even in the upper storeys, when there are such. Here and there the army disappears under the ground to come into view again a fair distance away. I have observed subterranean passages of this kind far away from any nest, and reaching as far as a metre down. In certain sheltered places, in grass, under stones, or in the trunks of fallen trees, the migrating Siafu can often be seen enlarging their road or covered path in order to lay their brood there for the time being. When part of a covered tunnel is destroyed, the Siafu do not rebuild it; they turn aside, even when the heat of the sun is fierce. We have seen that the ordinary hunting roads branch out, meet again and often form a network. The road on which the migrations are effected, on the other hand, is generally single and has no ramifications.

When the prey of the Siafu is large, it is immediately cut up into pieces for transportation, as we have seen, but in the case of small insects, etc., the legs and wings are simply cut off to prevent escape. The *Anomma* themselves have never been seen eating in the actual place where they are hunting, nor have the remains of their feast ever been

found on any of their roads. Every fragment is conscientiously delivered at the formicary, where it is eaten in common. The body of a victim is drawn so neatly that the portions connected by joints are dislocated and fall apart. Food-refuse is thrown out round the doors of the nest, where it is piled up and mixed with the building-earth. It is also possible for the Siafu to make some provision for times when they have to interrupt their hunting in the open. As to their subterranean activities, they are often revealed by earthworms which have been attacked by the *Anomma* in their earth-tubes, and although torn in pieces have managed to save themselves by emerging from the soil, whence they are not always pursued by their executioners.

While the prey is being quartered and the big columns are on the march, the rustling noise produced by the Siafu can be distinctly heard."

"The bite of the *Anomma*," continues Vosseler, "even that of the small ☿, is especially unpleasant and painful, though it is not intensified by any poison and consequently has not the excruciating results of other ant-bites. To be bitten to death by the Siafu must be one of the most cruel torments that can be imagined. The domestic animals of colonists, especially the small ones, such as fowls, often succumb to the attacks of the *Anomma*. Horses, donkeys and mules infested by them are infuriated and have to be set at liberty. Poultry-breeders often wake in the morning to find nothing left of their fowls and chickens but feathers and bare bones. At Tanga the people declare that a few years ago a captive leopard was killed and drawn in a single night by the Siafu. By preference these ants will first attack the delicate mucous portion of the eyes, nose, etc., and they always discover almost at once the most sensitive parts of the skin.

Their bite is rendered all the more painful by their instinct for moving their sharp toothed mandibles in the sore. Even when carefully delivered from their executioners and treated with the utmost care, small animals which are wounded in this way by innumerable bites will more often than not succumb. It seems to me that the recovery or death of the victim depends either on the amount of blood lost or on the extent of the cutaneous surface that is covered with bites. Hence I believe that the Siafu lick the blood of their victims when they cannot immediately tear them to pieces. When the hæmorrhage is too violent, or the bitten surface of the skin too large, the victim can no longer be saved: otherwise it may recover."

"The *Anomma* wage perpetual war with all animals. Their audacity, like that of the *Polyergus* (see Part IV, Ch. VII, 2), admits," says Vosseler, "of neither fear nor flight. Every creature that moves and has a heart that beats—be it large or small—is attacked by the Siafu with savage fierceness and blind, impassioned gluttony. This is literally true, for the *Anomma* are actually blind. The ☿, ♃ and ♀ have no eyes (their Greek name, *Anomma*, means 'eyeless': Forel). This fact renders the habits of the community and of each of its individuals still more wonderful than they are on their own account. Nevertheless, the Siafu seem to be delicately sensitive to light and dark, and therefore may be credited with a kind of light-sense. When a shadow falls upon an army marching in broad daylight, it soon grows uneasy and sends out emissaries. The ease and certainty with which the Siafu ant-population finds its bearings at relatively great distances, the regularity and order which prevail in its march along the roads, its changes of direction and deviations, the hunting of its victims and their quartering and removal, the pursuit of foes and

fighting with them, etc.—how all this can be accomplished by blind creatures is difficult to imagine. As is so often the case under such circumstances, the absence of sight seems to be compensated by a correspondingly greater development of the other senses, especially those of touch and smell. These sensory faculties, combined probably with a specially strong sense of direction, enable the Siafu to construct roads which in the most unsatisfactory districts may diverge as far as 10 or 15 metres from each other, to re-unite between 50 and 100 metres farther on; this enables individuals which have been separated a distance of 3 or 4 metres from the mass, whether by violence or not, to find their comrades safely once more, even in spite of the wind.

The fineness of their noses—in a figurative sense—renders the Siafu an inestimable service in the pursuit of their prey. At a considerable distance they perceive a scrap of meat which has been left in their domain. By means of a kind of intelligence or police service (antennal language: Forel), every individual is promptly instructed in any matter of interest to the whole family. Every disturbance in a column is immediately announced to the whole army, in front as well as behind, so that all round the threatened area the whole troop gathers instantly to strengthen the common defence. We can scarcely expect flashes of tender sentimentality in the minds of a fierce race of brigands like the Siafu. At the same time we cannot but admire the indomitable courage with which one for all and all for one in the ant-world will unconditionally sacrifice the individual life for the sake of the colony. The rapidity and good-will with which all the ☿ work to assist each other and share in every kind of labour—in a word, the high development of a mind entirely concentrated on the social

well-being of the community, cannot fail to fill us with amazement."

Indeed, after reading the above admirable description by Vosseler, which is as lively as it is fascinating and withal scientifically exact, we human beings, full as we are of cowardice, hypocrisy and bluster, can only bow our heads. But at this juncture certain important questions arise. Other authors have declared that monkeys, parrots and even large animals, when confined in cages or otherwise, are often killed in the night by the *Anomma* and reduced to skeletons by the following morning; these statements confirm those statements of Vosseler.

But what happens in the case of man himself? Like the large animals, he is not slow to run away when he is free and has the use of his hands to enable him to rid himself of the first Siafu which show an over-hasty anxiety to bite him. But I have read somewhere that if certain negroes wish to be revenged on an enemy, they will bury him up to his neck, covering his hands and feet, in order to have the savage pleasure of seeing him bitten by the Siafu and killed by inches as they gnaw his head. There is nothing impossible about this, and in view of the mentality of the negroes and of the *Anomma*, it is even quite probable. Nevertheless this story needs proper confirmation.

A second question which has long engaged my attention, and which Vosseler has now answered is this: How can an insect entirely without composite eyes and ocelli go hunting in the broad daylight and open air? *Anomma* is generally brown or black in colour, not yellow like *Dorylus* or the *Eciton* species which have no eyes and which hunt underground. Here I will refer the reader to Chapter I of Part II. One solution of the problem is that the topochemical sense of the antennæ is unusually well developed

in *Anomma*, and that this development is combined with an extremely correct instinct for discipline in its expeditions, similar to that of *Polyergus*. Or it may be that certain *photodermatic* sensations (perceptions of the intensity of light through the chitinous surface of the skin, that is, by its nerve-terminations) supplement the information provided by topochemical smell and antennal language which are finely described by Vosseler. My own experiments in former days proved that ants perceive with their composite eyes even the rays which we call 'ultra-violet' and which are not visible to us men. But these experiments did not exclude the photodermatic sensations that are known to be present in a number of the lower animals which have no eyes.

Long before the time of Vosseler, Savage (1874) described the habits of *Anomma*. "They come out," he says, "at night or on cloudy days. When they are detained by the quantity of their prey till late in the morning of a sunny day, they protect themselves by constructing arches of dirt agglutinated by a fluid excreted from their mouths.

When migrating, an arch is constructed of the bodies of their largest class (soldiers) . . . Whenever an alarm is given, the arch is instantly broken, and the ants, joining others of the same class on the outside of the line, who seem to be acting as commanders, guides and scouts, run about in a furious manner in pursuit of the enemy. If the alarm should prove to be without foundation, the victory won or the danger passed, the arch is quickly renewed, and the main column marches forward as before in all the order of an intellectual military discipline (innate, instinctive, we ought to add, without any previous drill: Forel)."

Savage divides the *Anomma* ☿ into three classes: (1) the ♃ (fig. 107 *C*) which are adapted to defence and attack and have mandibles with pointed teeth which enable them to

cut through an enemy's skin, hold the creature firmly and sap its strength; (2) an intermediate class of medium size (fig. 107 *D*, but often larger than the one shown in the figure), with less convex mandibles bearing well-developed, oblique teeth, whose function is to tear and cut up prey rather than to assist the ♀; (3) small ☿, with mandibles like those of the medium-sized ones, whose principal duty is to fetch and carry. At times, however, the rôles of these three classes are interchanged.

Savage saw a legion of *Anomma* encamped on a tree. From the lower branches, more than a metre high, there hung festoons of ants, an inch thick, reaching down to the plants and ground below. He saw one of these festoons in the act of formation. One after another, the ants came down from the top to the bottom, stretched their long legs, opened their mandibles wide, and fastened themselves to their companions, thus making the chain longer and longer until the bottom of it touched a broad canna leaf. The festoon swung in the wind, and the ant at the end strove in vain to get hold of this leaf. Presently Savage saw a ♀ climb up the leaf from below and fix his hind legs with the apex of the abdomen firmly upon it, beneath the vibrating column formed by its companions, which it seized with its wide-open mandibles, aided by its hind legs. Thus was completed what Savage calls 'the most curious ladder in the world.' Living chains such as these are used as a means of passage for an army, and also, as we have seen, to form a bridge for crossing streams.

Apart from the animals mentioned above, Savage says that *Anomma* attacks *Python natalensis*, the largest serpent in Africa, when gorged with prey, and cuts it up; it enters houses and attacks and destroys all vermin, including mice and rats. On certain occasions—rare it is true—their

visits may even be desirable. In that case, it is possible to save oneself by standing the feet of a bedstead in vinegar; this device is successful if the rooms, or at any rate the upper storeys, are well ceiled. Otherwise the ants will fall upon us, as on their noxious prey. If we destroy large numbers with boiling water, or bar their passage, they will abandon their project in despair, and explore some more congenial place. When they are fairly in, we leave the house at their disposal, apart from our beds and chairs, and await their pleasure; we may then have cause to be grateful for their services.

Savage tells us that *Anomma* love fresh meat and fresh oil but they will leave milk, sugar, pastry, and unboiled salt meat. Hence it is not true that they 'devour everything eatable,' as some writers have stated.

Anomma is unquestionably the most interesting of the visiting ants, and is only found in tropical Africa. Fig. 107 *A* represents the ♂ of *A. nigricans*, whose ♀ and ☿ are shown in *C*, *D* and *E*. This ♂, with its large eyes, can sometimes be seen on the march during migrations. Fig. 107 *B*, represents the enormous blind ☿ of *A. Wilwerthi*. The ☿ of *A. nigricans* is smaller. All these figures are slightly less than twice the natural size of *Anomma*. The ♀ and ☿ of *A. Wilwerthi* are slimmer than those of *nigricans*. The pangolin, a mammal with a scaly covering, feeds on ants, even *Anomma*; I have described how *A. opacus* was taken from the stomach of one of these animals. All the *Anomma* ☿ are blind and, like the ☿ of all the *Dorylinæ*, they have no wings.

In 1912 the German Vice-Consul, Schultze, sent me from Entebbe in Uganda, East Africa, some *Anomma* ☿ which he had taken, together with their brood, from the middle of their nest, or rather the lair of their robber ☿ and

♃, with considerable difficulty. These ants are accompanied in their migrations by their numerous guests or satellites of all kinds, which we discussed in Part II.

We must now pass on to other robbers which are more secretive if not more modest—*Dorylus*—and its sub-genera *Typhlopone* and *Rhogmus*. They are just as carnivorous and just as blind as *Anomma*, but they are yellow in colour and their much shorter mandibles are toothed, like those of the small and medium-sized *Anomma* ☿. They have no distinct ♃, but only large ☿ and they always hunt underground. often under sand, as we saw in Part IV, Chapter III, sec. 4,

In 1889 I myself observed at Sfax and the oasis of Gabès, in Tunis, the forays of *Dorylus* (*Typhlopone*) *fulvus*. At Sfax I only saw their results in the form of a number of corpses of *Cremastogaster* and *Dorylus* ☿. But in 1890 I gave the following account of my Gabès experiences to the Congress of German naturalists at Bremen:

In April, 1889, I had the opportunity of observing a *D. fulvus* (*juvenculus*) army which was carrying on an active war with beetles underneath a stretch of well-manured ground (Staphylinids, *Aphodius*, etc.) in exactly the same way as that described by Bates and Belt in connection with the American *Eciton*, save that as a rule *Eciton* hunts in the open air. When I put the whole collection of insects into a box and took it away with me, violent attacks on the part of the *Dorylus* against the others continued to take place even inside the box. I owed the discovery of these *Dorylus* to an old Arab who had sought my medical advice for a young negress, his slave. The wife of an Algerian guide afterwards told me how in June, 1888, a crowd of large 'bees' (*Dorylus* ♂) had come out of the interior of her house with some yellow ants, during a few days only, and had eventually flown away. These facts prove that *Dorylus* hunt and

build nests underground, in a secretive fashion, and are only seen at the period of the flight of the males.

I printed this account in detail in the journal *Humboldt* (Vol. IX, No. 9, 1890). For instance, some *Dorylus* seized hold of a number of *Aphodius* under my very eyes, and tore them to pieces in a rage; their antennæ were in perpetual motion. They were not in the least disconcerted by my interference, but they bit with all their might. Santschi, in 1908, confirmed my guide's statement. In a Tunis dye-works, one afternoon, at about 4 o'clock, he found a large *D. fulvus* formicary, whose ♂ swarmed in hundreds and spent six consecutive days in setting out on the wing. The dyer assured him that he had noticed the same thing happening, at the same season, about four years before. This, says Santschi, would seem to indicate that certain *Dorylus* may sometimes inhabit the same nest for a long time, instead of emigrating. Marshall and Brauns affirm that the ♂ of *Rhogmus fimbriatus* and *Dorylus brevipennis* are driven from the nest by the ☿ over a period of several days, and Wheeler assumes that this is so. It has been suggested that the males are adelphogamous, but in that case, what can be the purpose of their large eyes?

In 1880 my old school-friend, Paul Berthoud, who became a missionary at Valdezia in the Transvaal, South Africa, collected some interesting ants for me, including a specimen of *Dorylus helvolus*, which he sent me accompanied by the following letter:

"I had often heard of these ants in Valdezia; they were said to be in the habit of invading houses by night in serried ranks, and never to pass over a man's skin without biting it; it was also said that one had to resort to strong measures to drive them away (by thoroughly cleaning out their haunts, etc.). However, I had never seen them until

one evening my wife called me to her assistance, declaring that some little creatures were running over her legs and eating her. I ran to the spot. It was in the pantry, and there on the floor, level with the ground surrounding the house, the ants formed a compact mass. I had them swept away and removed as speedily as possible, placing the most attractive cluster in the flask which I send you."

Berthoud wrote to me later on in connection with another and similar case; he had been wakened one night by the cries of their child, whom he and his wife were only just in time to save from the bites of the *Dorylus*, out on a hunting expedition. It is a very curious thing that neither Santschi nor I have seen or heard anything comparable to this in either Tunis or Algeria. It seems, therefore, that in this region *D. fulvus* does not go hunting in houses, although it lives in them.

In India, morever, the *Dorylus* of the sub-genus *Alaopone* (*D. orientalis*) appear to be herbivorous, not carnivorous. According to Green, they eat the bark of trees and various tubers, such as potatoes. This statement requires confirmation, though Green is a good observer, for, if accurate, it forms the only known exception among the *Dorylinæ*. I know of no observations on the habits of the sub-genus *Rhogmus* of Africa, apart from the fact that Marshall discovered the nest of *Rhogmus fimbriatus* with a ♀ and a few ♂, not to mention the ☿. The habits of sub-genus *Dichthadia*, of the Sunda Islands, are equally obscure.

With regard to the nuptials of *Dorylus* and *Anomma*, nothing positive, so far as I know, has yet been observed. The ♂ fly away; but where they go, and where and how they attain their wingless ♀, is still a mystery.

Thus we come to the second tribe, that of the *Ecitini*. All the *Ecitons* and their sub-genera live in America. Fig. 108

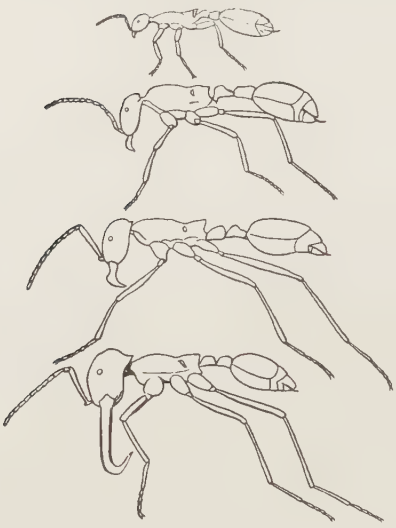


Fig. 108

represents, beginning from the top, three worker-stages in *Eciton hamatum*; their mandibles grow longer as their bodies grow larger, until finally they are like those of the ♀ drawn in profile in the fourth line, at the very bottom. Fig. 3 *B*, in Part I, gave a front view of these curious mandibles, which form two long, narrow, toothless hooks, incapable of biting except with their sharp, inward-curving point. Mandibles like this are only present in a few *Eciton* species; most of them have no distinct ♀. Several species have a large ocellus on either side of the head, replacing the ordinary composite eye (Fig. 108 and Part I, Chapter III).

In 1863 Bates, in *The Naturalist on the River Amazon*, gave us our first precise account of the habits of *Eciton*, or the *Taucca* of the Indians. He took ten species, each with some peculiarities in its habits. *E. rapax*, the giant of the genus, has no distinct ♀, and its armies, which are not large, consist each of a single file of workers. According to Bates they seem always to attack the same specimen of ant, probably a *Camponotus*, which they tear to pieces and eat. *E.* (*Acamatus*) *legionis* is small, but it moves about in broad daylight in columns of thousands. Bates saw it attack the nest of a large *Camponotus*, killing and quartering the inhabitants and the brood under his very eyes, and even

snatching them from his fingers when he had broken into their nest with his spade. In two hours' time they had ravaged everything and killed, quartered and carried away all their prey, as *Anomma* will do. Bates thinks that the hooked mandibles of the ♀ of *E. hamatum* are only used to wound the stomachs or tongues of ant-eating birds and mammals. This is very likely, and I myself formed a similar hypothesis with regard to *Machæromyrma* and the spines of *Polyrhachis*, without knowing anything about his species; but, all the same, I think that they may have other functions similar to those of the *Anomma* ♀.

Bates tells us that *E. hamatum* marches in dense columns, consisting of countless thousands of individuals, followed by birds. If a man goes near them they climb up his legs and bite furiously, so that he has no alternative but to escape. They hunt in the thickets of the tropical forest, and wherever they pass we find alarm and flight in the animal world, especially among spiders and wingless insects, ants of other sub-families, etc. Like *Anomma*, they do not climb high. The principal column forms a front 4 to 6 metres wide and clears the ground of all animals, living or dead, meanwhile sending out small lateral columns upon its flanks, to forage. If, for instance, it should discover a decayed tree-trunk full of larvæ or some other likely object it stops, closes its ranks, penetrates every corner and tears to pieces every living thing, as *Anomma* does, and with no less fierceness. It even attacks carton wasps'-nests, built on bushes. The ants tear the carton and drag out the nymphs of the wasps and pull them to pieces, heedless of the anger of the adult wasps, which fly all around them and would be killed themselves if they ventured to settle. The dissected fragments are divided among the ☿ according to their size, the smallest ☿ carrying off the minutest pieces; the ♀,

however, take no part in this. Bates was never able to find an *Eciton* nest, and never saw this species except on the march. Nevertheless, in a corner of the forest, pierced by the sun's rays, he saw them resting, brushing and combing each other's limbs.

Eciton prædator does not march in columns, but in a thick phalanx consisting of myriads of individuals, which even climb on to the leaves of bushes. Bates tells us that these phalanxes occupy about 5 square metres, and, viewed from near at hand, consist of several columns.

Eciton crassicorne sometimes builds vaults—when, for instance, it has to cross an uncovered road. Bates describes the arches made of dirt (like those of *Anomma*) by *Eciton* which are totally blind. Here it seems to me that the deplorable descriptions of F. Smith led Bates to confuse *E. cæcum* and *E. prædator*.

Belt, in *The Naturalist in Nicaragua*, 1874, completes the picture. He says that the greatest catch of the *Eciton* is to get amongst fallen brushwood. Instead of running right away, cockroaches, spiders, etc., would ascend the branches, whither the ants follow them, and lay siege to their base, —eventually killing them all and pulling them to pieces, with the exception of a few spiders, which, more wily than others, let themselves fall halfway down and hang by threads. Being artful and wary, morever, these spiders foresee danger and flee to a great distance without stopping, instead of hiding directly the first wave of excitement is over, as insects do. Nevertheless, Belt saw a green grasshopper, a perfect imitation of a green leaf, remain quite motionless amid some *Eciton*, which did it no harm. He even managed to take it and place it on the ants, without causing it to make any movement. The *Eciton* did not perceive it, either by sight or by smell. Perhaps we have here an indirect

confirmation of paroptic vision, for *Eciton prædator*, the species in question, has only two very small eyes which are almost atrophied! By this means, the grasshopper was at the same time instinctively protecting itself from the thrushes which follow the *Eciton*, not for love of them, but in order to snap up the prey that flees before them, as Bates and Belt have shown.

Belt saw only one other ant, a very peaceable and cowardly *Dolichoderus*, being attacked by *Eciton* (*E. hamatum*). They did these ants no personal harm, as all they wanted was their brood, which they cut to pieces while plundering the nest. Belt regards the ♃ of *E. hamatum* as officers directing the march of the column; hence he agrees with Savage and Vosseler in all matters concerning the *Anomma*, and not with Bates. Probably a combination of both views would give us the truth. Belt furthermore believes that *Eciton* sometimes attacks birds' nests as it does wasps' nests. This author also experimented with the trail of *Eciton* which were following one of their scouts on dry clay. He removed part of the clay bearing this trail, upon which the *Eciton* stopped on both sides and wandered round in circles until they found the scent by swerving to the other side of the gap. They immediately recovered their confidence and went forward again.

Belt was the first to discover a provisional *Eciton* nest, the species being *E. hamatum*; he did not think that it had endured for more than four or five days. These nests are made in hollow trees, and sometimes underneath large fallen trunks. He saw one about a cubic yard in bulk, containing hundreds of thousands of individuals, huddled together in a living ball pierced with tunnels, also living, which provided passages for the ☿ laden with pupæ or prey. Belt thrust his stick through one of these clusters, and when

he drew it out ☿ laden with larvæ and pupæ were hanging from it; and he found that he could be severely bitten by the ♃. The removal of the whole colony, which may include a million individuals or more, is directed by the ♃. On either side of the column of workers, bearing their brood, ♃ march in front and behind, to preserve order. According to Belt, the distance between the old station and the new may amount to 200 or 300 metres; but he discovered no *Eciton* ☿ or ♂.

Belt made some more experiments, however; for instance, he put a pebble on the back of a ☿, and admired the perseverance with which her companions strove to free her from it. He noticed the signals of the antennal language, and the manner in which the ☿ thus called for help and succour. But it seems to me that Belt confuses instinct and individual memory. Here I will refer the reader to Chapters I and II of Part II. Finally he compares the social system of mutual help among ants with Sir Thomas More's *Utopia*.

For the first identification of the *Eciton* ♂ with their ☿, we are indebted to Hetschko and W. Müller. Before their time the two forms were attributed to different subfamilies, owing to the fact that the ☿ has two joints to its pedicel and the ♂ only one. But the decisive biological observations were made by Müller. A few days before, some *Eciton Burchelli* had invaded and stripped the house of his brother, the famous Fritz Müller, at Blumenau, Prov. Sta. Catharina, Brazil. On February 28th, 1885, at 9 o'clock, W. Müller saw a serried column of these *Eciton* bearing their brood, including woven cocoons, larvæ, etc., in the garden. A few paces away the column settled on the branches of a newly-felled tree. W. Müller examined the tree thoroughly and discovered in it a great legion of *Eciton*, with all their brood; they were all heaped up in

large bundles in the open air, almost like those mentioned by Belt, but divided into three and provided with a surface-covering of ♀, the ☿ and the brood being inside; the larvæ were mingled with the woven cocoons. But by 10 o'clock at night the scene had changed: a powerful *Eciton* column laden with brood had set out on the march, and began very hurriedly to migrate. At 11 o'clock W. Müller returned and saw hundreds of *Eciton* pass by in one minute, similarly laden.

Next day, the first of March, at 6 o'clock in the morning, the migration was still continuing, though it was slackening; at 7 o'clock, a few more larvæ passed by; then all was over. The column of *Eciton* climbed up a slope covered with ferns in the undergrowth of the forest, and 200 paces further on came to the hollow of a fallen hollow tree, into which they poured with their brood. From this spot Müller saw another column of *Eciton*, this time without brood, but laden with prey and arriving at the nest from the opposite direction. On February 28th, therefore, there had been but a single temporary halt during the day, and this was a migration which must have begun on the 27th. But the nest at this halting-place still contained brood; in the evening of March 1st some *Eciton*, checked by the sun, took up the rest of their brood in order to carry it to the new nest. It was at this moment that Müller found among the *Eciton* an *E. Burchelli* ♂, accompanied by two ☿ which were driving it along. This ♂ was slightly wounded, and had only the stumps of the wings. Thus it was that Müller proved the identity of the ant formerly known as *Eciton Foreli* (Mayr) with *Labidus Burchelli* Westwood!

Müller also found the nymph of a small ergatomorphous (wingless) ♂ of *Eciton Burchelli*, which he sent me to dissect. He followed the peregrinations of these ants until

March 17th, but could not discover the ☿. After Hetschko, several people, including Wheeler, succeeded in finding the ♂ and ☿ of *Eciton* together.

André (1885) quotes a passage from Bar, who once, when he was near Cayenne, met a column of *Eciton hamatum* crossing a column of *Atta cephalotes* (leaf-cutting ant) by passing over it on a piece of wood, which served as a bridge. Bar says:

"A malicious idea entered my head — to remove the piece of wood on which the *Eciton* were passing. A terrible confusion ensued. The individuals with long mandibles (♀), which seemed to have some kind of authority, turned hither and thither, from one side to another; the others stopped in front of the obstacle presented by the *Atta*. But, by a happy chance, a small piece of wood, as large as the shaft of a feather, was revealed a few centimetres away, and advantage was taken of it. It was too thin and the passage was too narrow, but this obstacle was quickly overcome. Ten, twenty, fifty individuals clung to either side of it, in two rows, and thus the path became wide enough to enable the column to pass over a living bridge.

But the curiosity of the entomologist is insatiable. I destroyed this new bridge to see what limits there would be to the courage and intelligence of the one species and the perseverance and tenacity of the other. This meant fresh confusion! Unfortunately there was not another piece of wood in the neighbourhood to replace it. The confusion increased: a compact mass of *Eciton* found itself at a standstill before the column of *Atta*, which it had to cross under pain of seeing its line broken. This it did resolutely, and the disorder reached a climax. The largest *Atta* continued to cross, but the smaller ones were knocked over, and their bodies lying upside-down formed still another obstacle.

Finally, our *Eciton* made a supreme resolve. Suddenly, as though at a given signal, a multitude of individuals, over an area of 20-30 millimetres, flung themselves to the ground and clung to the soil with their long legs, arranging themselves in several rows; others mounted on their backs to form a second and then a third storey, and two walls were thus formed simultaneously, 5 or 6 centimetres away from each other. The column then passed over in triumph, while the *Atta* scattered in every direction, unable to rally."

It was I myself who discovered the first fertile *Eciton* ♀ alive in her nest. At the end of July, 1899, I found time to examine at my leisure a pine-wood in North Carolina, U.S.A. There I discovered in a decayed trunk the nest, or rather provisional camp, of a colony of the small *Eciton* (*Acamatus*) *carolinense*. This species is blind, and its nymphs are naked, as I was able to prove. The trunk was literally impregnated with *Eciton* ☿, to a distance of 3 centimetres above the soil and the same amount below. Making up my mind to find the ♀, I ruthlessly destroyed the whole tree-trunk from top to bottom with my chisel, spreading all the brood round me. I was beginning to despair, when, among the wreckage, I caught sight of a large live creature moving among the pygmy ants. This was the ♀ of my search, the mother of the rest. I jumped with joy. This ♀ had an enormous abdomen, but no eyes or wings, and she could scarcely walk. The *Eciton* nest had neither chambers nor galleries; the ants with their brood had simply made their way into the rotten substance of the old trunk. I gathered many of them into a bag, in order to use them for some experiments. Directly the ☿ came out of the bag, scarcely five minutes later, in a strange place—a garden in Washington—they managed to act on a concerted plan, form files, follow one another swiftly and find their way to explore the

grounds together. I have never seen such a thing happening with any other ants, and I was thunderstruck.

Apart from this, I have had no opportunity of studying *Eciton* in America. I met one column of *E. hamatum* and one of *E. Burchelli*, undoubtedly on the march, but bearing neither brood nor prey: no birds were following them, no insects fleeing before them, and they made no attacks, but rather appeared to be strolling about in *dolce far niente*. The *E. hamatum* were even driven back by some *Azteca*, which sprinkled them with poison from their anal glands. Similarly, all that I could personally discover about *E. prædator* was that it had arches built with earth.

Dr. Bruch, of La Plata, wrote me that he had observed an army of large *Eciton quadriglume* attacking some *Mœllerius Silvestrii*. The *Mœllerius* emerged in a mass and defended themselves bravely, seizing a large number of *Eciton* by the legs and pinning them to the ground. Hundreds of *Eciton* were checked in this way. Then night fell, and Bruch was unable to continue his observations. He had also discovered the large ♀ of *Eciton* (*Acamatus*) *Strobeli* and that of *Eciton* (*Labidus*) *prædator*—both of which he has described and depicted in his *Estudios mirmecologicos* (1921). More recently Wheeler, in Guiana, found the queen of *Eciton Burchelli*, entirely covered over by a legion of workers.

Schmitt (and Wheeler after him) found more *Eciton* ♀, some even in company with the ♂. Wheeler has made some interesting observations on various *Eciton*. He saw the ♂ of *E. Schmitti* flying away alone, like the ♂ *Dorylus* in Tunis, and proved that the *E. cæcum* ☿ is very fond of eating nuts. I, like Wheeler, only saw this species underground, and could not find its nest. Prof. Bugnion brought me from Venezuela specimens of *Eciton crassicorne* which were having a furious fight with some *Cephalotes atratus*, against

whose hard carapace their mandibles and stings were powerless. I suppose they coveted the *Cephalotes* brood. As early as 1868 Sumichrast had made some excellent observations, similar to those mentioned above, on the Mexican *Eciton*.

Nothing is known about the habits of the *Cheliomyrmex* of America or the *Aenictogeton* of Africa.

Next comes the genus *Aenictus*, which is common in Asia, Africa and Australia. My friend Wroughton, in 1892, was the first to discover their ♂ being driven from the nest by the ☿. This destroyed the myth of the genus *Typhlatta*, which Smith founded upon the ☿ alone, and which proved to be a simple synonym for *Aenictus*. Wroughton, who has observed *Aenictus* in India, declares that their habits are much less subterranean than those of *Dorylus*. They bear their prey, so he tells us, exactly as the *Ponerinæ* do, and their military organization is perfect. Their diminutive size (scarcely 2 or 3 millimetres, rarely more) prevents them from allowing their discipline to slacken. That is the reason why a column of *Aenictus*, with a front of five or six ☿, whatever its length may be, never shows the least irregularity. The *Aenictus* have no scouts. The ☿, which are all of the same size in every species, march in a long, swinging trot, until they discover some little crevasse or a subterranean ant-nest, which they invade until no more ants can enter; the rest then go in search of other prey. Sometimes the column turns off at an angle and changes its direction, but Wroughton never saw it grow weaker or break up into several files. It is obliged always to be strong enough to fight any other ant-community it may meet. Nevertheless, Wroughton saw a strong column of *Aenictus*, on the march towards a termite-dome, detach columns on its right and left flanks to invade this dome from different

sides at the same time; manœuvres like this, he observes, give the impression of being preconceived or commanded. *Aenictus* is entirely without eyes.

Brauns, in Africa, has made observations similar to those of Wroughton. He says that *Aenictus* avoids the light of the sun to a much less extent than *Dorylus*. At dusk, or on a rainy day, sometimes even in broad daylight, they will

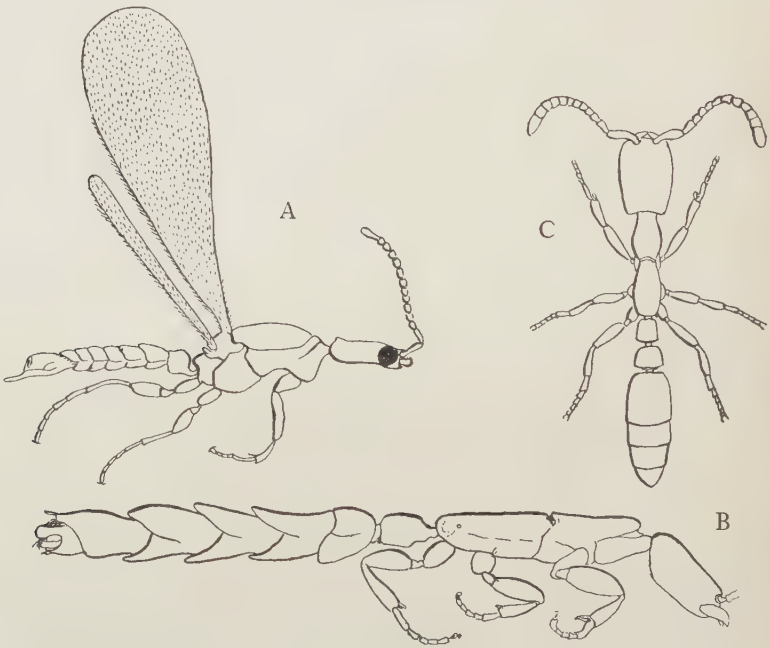


Fig. 109 A B C

march for a long time in the open. Their files resemble those of *Anomma* in miniature. Their columns are very regular, in Africa as elsewhere. Brauns saw them carrying their brood between their legs in the manner of the *Ponerinæ*, and I may add, of *Polyergus* (see fig. 106 *A* in Part IV): I have made the same observation with *Eciton carolinense*.

Finally, we come to the last of the pygmy tribes, the *Leptanillini*. This genus Leptanilla, discovered in Corsica by Révélière and described in 1870 by Emery, who also proved that it belonged to the *Dorylinæ*, possesses, with *Oligomyrmex*, the smallest, and more especially the thinnest, ants known anywhere in the world. Their blind ☿ are about a millimetre long, and extraordinarily narrow. Fig. 109 represents in *A* the winged ♂ with his large eyes, thin head and wings without neuration, in *B* the blind and apterous ♀, which has only one joint to her pedicel, and in *C*, the worker, which, like *Eciton* and *Aenictus*, possesses not only a petiole, but a distinct post-petiole, entirely separate from the abdomen.

They were discovered hidden under stones or amongst dry leaves; the ♂ were taken by lamp-light, and discovered by Santschi in Tunis. One species has been found at Singapore.

Everything points to the belief that the *Leptanilla* hunt the most minute live creatures, such as mites.

There, friend reader, we at last bid farewell to the wars waged by ants, and also to their nomad and sanguinary tribes, and turn our attention to the peaceful industries, agricultural and otherwise, that are carried on by certain tribes of our little friends.

Chapter II

THE GRANARIES OF HARVESTING ANTS

Whether you are a believer or an unbeliever, dear reader, and it is immaterial to me, I beg you to peruse the following passage from the Bible, *Proverbs*, Chapter vi, 6: 'Go to the ant, thou sluggard; consider her ways, and be wise; which, having no guide, overseer, or ruler, provideth her meat in the summer and gathereth her food in the harvest.'

And then again, Chapter xxx, verse 24: 'There be four things which are little upon the earth, but they are exceeding wise; the ants are a people not strong, yet they prepare their meat in the summer (the coneys . . . the locusts . . . the spider. . . .).'

Solomon saw more clearly than certain scientific men, who were prejudiced, and would not believe that the ants of Palestine were distinguished by their habits from those of their own countries. Emery has shown, moreover, that it is not for their almost non-existent winter, which they do not spend in sleep like our species, that the harvesting ants gather seeds in their granaries, but for the dry, hot season in which they can find nothing to eat.

Furthermore the writers of antiquity, Hesiod, Horace, Virgil, Plautus, etc., have made many allusions to the granaries of the harvesting ants, and Claudius Aelianus (*De Nat. Anim.*) even gives an excellent description of their habits. But here, you see, the human mania for generalizing everything that is observed has caused the northern authors

to generalize septentrional winter sleep, and the southern authors to generalize harvest-granaries, as peculiarities of all ants. In 1747, however, Gould saw the truth of the matter, and predicted that ants of hot and cold countries would prove to have different habits. This was very well expressed in 1873 by the English writer, J. Traherne Moggridge, in his book *Harvesting Ants and Trap-door Spiders*, wherein he gave us the first scientific biological study of the harvesting ants, which he studied at Mentone, in the South of France. In Europe, this speciality is represented chiefly by *Messor*, discovered by Moggridge, *Oxyopomyrmex* and *Goniomma;* in America by *Veromessor* and *Pogonomyrmex;* in Asia by *Holcomyrmex* and *Pheidologeton;* and lastly, everywhere by a number of *Pheidole* and a few *Solenopsis* and other genera, all of which, apart from one or two exceptional cases, belong to the *Myrmicinæ*. Sykes (1829) and Jerdon (1851), investigating in India, were the first modern naturalists to see ants dry the seeds they harvested.

At Mentone, Moggridge observed three species of harvesting ants; two varieties of *Messor barbarus*, in which the head of the large ☿ is black and red respectively, *Messor structor* and *Pheidole pallidula*. He conducted his observations, especially those on *Messor*, in a valley near his home, between October 29th, 1871, and May 4th, 1872. For instance, a double file of *Messor* appeared travelling a distance of about 22 metres, between its nest and the wild grounds which were full of troublesome grasses, some barren, others laden with ripe seeds which were falling, their capsules still green. One ☿ climbed up the stem of a plant, a lavender, let us say; there she chooses a calyx whose base seems ready to let the seed fall at the first tremor. She then seizes the stem of the calyx with her mandibles, sets her weight upon her back legs as upon a pivot, and struggles to saw through the fibres of

the stem, working all round it until at last it is detached. She then takes hold of the detached calyx and walks patiently down the plant with her often heavy and cumbrous burden, crosses other stems and regains her companions as they return to their nest. It is one of these ants

Fig. 110

that you see faithfully represented in fig. 110 : She is carrying a seed, still covered by its husk. In 1883, at Château d'If, near Marseilles, I myself made observations upon *Messor barbarus* similar to those of Moggridge. This author never saw *Messor* cut off the stem of the seeds simply and cleanly. On the other hand, he saw two ☿ combining

their efforts, one sawing and gnawing the stem at its point of maximum tension while the other turned the calyx round and drew it towards her. As early as 180 A.D., Aelian gave a similar account of the way in which *Messor* detaches from their bases the husks of all the seeds of an ear, in order to bring them down and bear them to her nest.

On examining carefully the materials collected in this way by *Messor*, we find that the great majority of the ☿ bear back to the nest various kinds of seeds which they have either plucked as we have just seen, or found where they had already fallen. Some, however, bear other mixed materials ; a dead insect, a broken shell, the corolla of a flower, a chip of wood, a leaf, etc. Here I may add that the seeds whose stems are sawn through by *Messor* are not always ripe ; I have seen them bring back some which were still quite green. When they make a mistake and bring objects of no nutritive value, their companions throw the fruit of this useless toil out of the nest, or force them to throw it out themselves.

In this connection, Moggridge made the following experiment to find out whether *Messor* could really be deceived, like the generality of mortals; he took with him a small packet of white china seeds, which he sowed about the path of the *Messor*. Sure enough, a minute later a large ☿ seized one of these, after much effort, lifted it and returned quietly to her nest with her burden. Others tried to do the same, but in vain, and they presently perceived their error and left the china seeds alone, refusing to touch them any more. Moggridge often amused himself by scattering near the *Messor* nest seeds of hemp, oats, etc., of which they are very fond, and watching how eagerly they picked them up and carried them to their nest. Next day he was interested to find the empty coverings of these grains on the kitchen midden which covers the dome of the nest. Sometimes, after

a shower, the *Messor* may be seen dragging out of the nest any seeds which are beginning to germinate, and leaving them to dry in the sun.

All round the dome and the refuse-heap, Moggridge tells us, we frequently see plants grown which are altogether strange to the ordinary monotonous flora of the wild ground. They have sprung up accidentally from seeds brought from a distance by *Messor*, sometimes, for instance, from a cultivated terrace on which lemon-trees are growing. These patches of foreign vegetation reveal from afar the presence of a *Messor* formicary. Sometimes the rain washes away seeds of this kind into the miniature ruts or cracks in the rocks, where you afterwards find them growing.

Messor barbarus and *structor* construct no masonry domes. They content themselves with digging in the earth which they then throw out in the form of a crater, whether mixed or not with the refuse of their granaries, including the empty capsules. These craters and heaps of refuse may attain considerable dimensions wherever they are not dispersed by the wind and rain. While some of the ☿ are out foraging and harvesting, others are working in the nest, cleaning seeds and throwing all that is useless among the refuse.

Moggridge thus became convinced that under the *Messor* nest there must be stores of seeds, in other words, granaries. His first attempt at digging them up was vain, for he found nothing. He then dug into another nest stretched on a rock in a long horizontal line. This time, a short distance down, he found a granary in the form of a horizontal and more or less cylindrical gallery, very neatly laid out and full of amaranth seeds, black and shining like gun-powder. The floor of this granary was different from the surrounding soil, for the ants had lined it with grains of

flint and mica. On looking at it closely, moreover, Moggridge found not only amaranth seeds, but those of eleven other species of plants, belonging to seven families, in the various granaries of this single formicary. These granaries were situated from ·5 to ·6 inches below the surface of the ground ; they were all horizontal, and on an average each was as large as a watch.

Though they were all damp, none of these seeds showed the slightest trace of germination. Between October 29th and May 5th Moggridge thus gradually gathered seeds from twenty-two different *M. barbarus* formicaries. Among these thousands of seeds he only found twenty-seven, from seven different nests, which showed unmistakable traces of germination between November and February; the radicles of eleven of these had been bitten off by the *Messor*. He thereupon concluded that ants must have a hitherto unknown faculty of arresting a seed's tendency to grow, though in this he was contradicted later, chiefly by Emery and Neger. He proved that seeds which are removed from the granaries of *Messor* and planted in the earth germinate and sprout without losing any of their vitality. He also observed, in connection with natural nests and also with captive formicaries in apparatus, that the *last* seeds gathered before rain, or given to ants before they have been artificially damped, are the first to be put away to dry. Moggridge thinks that the seeds are usually softened and made ready to germinate before they are eaten. When seeds begin to germinate in the nest the *Messor* check the process by gnawing off the radicle, and especially by putting the seeds on the dome, to dry in the sun, and removing them as soon as they are dry enough.

From his observations Moggridge concludes that what occurs here is a transformation into sugar of the starch

contained in the seeds, like the transformation of barley into malt. He saw the eagerness with which ants devour seeds of this kind. It is unquestionable, he declares, that the great mass of seeds remain in the damp heat of the nest without either germinating or rotting, often from October to May, for there are some which cannot possibly have been gathered before October or November, and which are found intact in the granaries in May. He puzzled as to why they do not germinate simultaneously at a fixed time, as in the natural state in the earth, instead of waiting patiently to be eaten, though they can grow directly they are sown !

Moggridge counted thirty-five different species of plants whose seeds have been thus gathered by the *Messor* of Mentone. Dr. Bornet, of Antibes, he adds, complained of the havoc wrought by these ants among the seeds of exotic plants in the gardens of a rich villa. In some of their granaries at Hyères such quantities of cereals have been discovered as might have caused serious losses to farmers. Moggridge estimates the average amount of seed contained in the granaries of a single formicary at half a litre.

Messor structor loves to dwell in the immediate surroundings of human residences, where she can lie in wait for seeds, even those which are given to canaries. Moggridge found her at Mentone in a corn-chandler's shop. I myself have seen her swarming in the streets of Smyrna, and Prof. Bugnion has just sent me a few of her kind which were swarming through the cracks in a chimney at Aix, in Provence. *M. barbarbus*, on the other hand, lives in uncultivated places. According to Moggridge, the granaries of *M. structor* are laid out in the same way as those of *M. barbarus*. I saw some *M. structor*, which I had placed in an apparatus, continually turn and re-turn their seeds between their mandibles, but I did not see them eat or cut

them—though for that matter, my observation was very incomplete.

Moggridge says that the granaries of *M. barbarus* are situated from 1½ to 20 inches beneath the earth of the dome. I discovered some at the Bosphorus which were still more deeply sunken in the earth. Moggridge twice observed *M. barbarus* nests built in the crevices of a solid rock. With the aid of a friend, armed with a hammer and a chisel, he succeeded in tracing these *Messor* nests by breaking the rock to a depth of about 45 centimetres. There he discovered tunnel-like galleries, and also the enlarged portions forming the granaries and containing the winged sexes. He also found a kitchen-midden. In another place Moggridge discovered in a *M. barbarus* nest some curious little semi-circular vaults, regular and well-rounded, pierced by openings and serving as granaries. This had probably been in the first place the work of a scarabæus, annexed and transformed into a granary by the *Messor*. In these granaries Moggridge, like myself, found some *Lepismæ* and other ant-guests, such as we discussed in Chapter IV, Part II.

He also discovered small Cynipid galls (galls from which a small winged insect comes forth) in the granaries of some *Messor* which had probably gathered them by mistake, supposing them to be seeds.

Messor scarcely ever attacks other ants, and usually flees before them like a coward, even before the little *Pheidole*. On the other hand, her various formicaries engage in battle with each other in order to carry off seeds. These wars may last for several weeks. Moggridge observed a fight between two colonies of *M. barbarus* which scarcely flagged at all from January 18th to March 4th. The nests of the two formicaries, situated on a slope, one high up and the other lower down, were linked by a chain of ants bearing seeds,

over which they quarrelled. Those of the higher nest (*A*) won the day, forced their way into the lower nest (*B*) and stole the seeds it contained. But their opponents struggled to have their revenge, and a few daring spirits even entered the higher nest to recover their property. The *A*'s had organized a kind of customs-house round the doors of nest *B*, and when a ☿ returned with a seed thus recaptured the customs-officers took it from her and carried it back to nest *A*. Moggridge saw seeds being dragged in different directions by the ☿ of the two sides. He also saw ants whose limbs and abdomens had been cut off by the enemy, but which continued none the less to fight and hold fast to their seeds, etc. On March 4th hostilities ceased, but the *B*'s had not abandoned their nest.

On another occasion of the same kind, the fight lasted for 31 days and the victors entirely abandoned their nest; he found the chambers empty and the granaries completely rifled, all except one which had been obstructed by roots and therefore long neglected by the ants. It is strange that none of the seeds contained in this neglected granary showed any sign of germination. He thought that these forays were due to hunger, at the time when the young need food, for the ☿ could be seen staggering forth to such undertakings while still half-paralysed by the cold and rain. The swarming-time varies a good deal between November and March for *M. barbarus* and between February and April for *M. structor*. This must be understood to refer to the neighbourhood of Mentone, where Moggridge made his observations.

Although *Messor* lives normally on seeds, in times of dearth she devours dead insects, like grasshoppers or the larvæ of wasps and bees; Moggridge noticed this even with his captives in the apparatus. For instance, he saw them attack a large live caterpillar.

He established a colony of *M. barbarus* in a primitive apparatus of the Huber type, I imagine, with some earth, which they dug, and in which they constructed craters and granaries wherein to take the seeds given them by the observer. There they formed a refuse-heap for the seed-capsules, fed their brood, set the germinating seeds out to dry, etc., as in natural formicaries. He even saw them remove a few young plants sprung from the seeds which had succeeded in germinating and which, in growing, had pierced through the earth as far as the *Messor* galleries. Two ☿ were working upon it, one drawing the free end of a root towards her and the other gnawing its fibres in the strongest part. Once, too, he saw a *Messor* ☿ carry a sick companion to the water and, instead of throwing her in as usual, immerse her for a minute, then carry her laboriously into the sunlight (a bath followed by the sun-cure—the latest in human fashions!)

Moggridge used his captives to discover how *Messor* removes the envelopes (hardened skin) of the seeds themselves, which swell when they are on the point of germinating, as he had formerly observed her removing their capsules. These envelopes are removed before the seeds are eaten. Last of all he observed how these ants eat the contents of their seeds. Despite all his precautions, his captives avoided the glass and showed a preference for working in the earth. In the evening, however, they came out in a crowd to enjoy the heat and light of the lamp, and then, with the aid of a magnifying-glass, with great care, throwing a ray of light upon them, he managed to see them eating. Two or three ☿ at the same time were scratching the farinaceous portion of a millet-seed with their teeth and mandibles, and then catching the fragments in their mouths. To feed their larvæ, the *Messor* ☿ detach portions of seeds, which they bear

into the nest. However, Moggridge has never succeeded in finding starch in the stomach of a dissected *Messor*, even with chemical reagents (iodine).

He managed to induce some *Messor* to eat the starch which he obtained by breaking seeds for them. The flour was eaten when it was soft or oily, but thrown on the midden when dry and hard: he points out that the softening may be produced by water or oil indifferently. He also persuaded his captive *Messor* to eat a little honey, but they did not care for it very much and made no attempt to milk either the aphids or the coccids he gave them. Moggridge proved, furthermore, that *Messor* and *Pheidole* often go harvesting when it is absolutely dark. Before his departure in May, Moggridge examined the nest of his captive *M. barbarus* and found the formicary and its granaries, which were fairly tightly packed, everything being in perfect condition. In spite of the damp none of the seeds had begun to germinate.

Moggridge found no very marked difference between the harvesting methods of *M. structor* and those of *M. barbarus*, but says that *Pheidole pallidula*, on the other hand (he wrongly mentions *Ph. megacephala*, which is not found in France), does nearly all her gathering at night, and does not begin harvesting until April. But he did not succeed in disclosing their granaries. In my opinion our *Ph. pallidula* is only a partial harvester. What Heer proved for *Ph. megacephala* at Madeira is true of all these omnivorous ants: the ♃ function as carvers of all booty, animal and otherwise, using their sharp mandibles.

Moggridge also mentions *Lasius emarginatus*, *Tetramorium cæspitum* and even *Serviformica fusca* as seed-bearers under exceptional circumstances. In July, 1872, near Martigny, I myself made the following observation with a *Lasius brunneus* colony whose nest, situated under some

stones which stood close against the foot of a walnut-tree, was continued into the earth round the roots and into the bark of the trunk. In those nest-chambers which lay under stones a considerable quantity of small black seeds, oblong and hard, with white, soft hila, were heaped together. They were about the size of millet seeds, and were neatly arranged in heaps proportionate to the height and the surface of the chambers, as in the *Messor* granaries. The ☿ of *L. brunneus*, which, however, lives for the most part by her aphids, were bearing these seeds like their own cocoons, which were not found under any other stones, but only in the *Lasius* chambers. I have never seen such a state of affairs again, but it seems obvious that this was a granary—a thing quite exceptional in this species.

Moggridge furthermore quotes an observation made by Mr. Horne in November, 1866, at Mainpuri in India, with some *Sima rufonigra*. Horne describes how these ants, which have their nests in the earth, gather grain and make granaries very much as do the *Messor*.

Since that time, dear reader, no observations on the harvesting ants so complete, conscientious, and patient as those of Moggridge have been made, and I am aware that I myself, during my numerous travels, have been very superficial in this respect, compared with him. But he only worked at Mentone and by no means exhausted the subject, as he says himself and as we shall see; and my only excuse is that there are no harvesting ants in the canton of Vaud: I have had no opportunity of seeing them except while travelling.

One thing which has always interested me is the fact that the mandibles of the large ☿ of the large harvesting ants, especially in *Messor*, *Pheidologeton* and *Holcomyrmex*, are so worn and obtuse at their terminal edges during old age, whereas teeth are still present shortly after hatching. This

seems to me a clear proof that the task of cutting seeds devolves mainly upon these largest individuals with their enormous heads, who on the whole very seldom leave the nest. Even I myself, while passing through Algeria and Tunis, have observed wars between *Messor* colonies, the undoubted purpose of which was the rape of seeds.

Emery repeated Moggridge's observations, using an up-to-date apparatus on the Janet system, in which he could watch the ants eating. The large ☿ do really grind up the seeds and reduce them to paste or soup with their saliva before swallowing them. Their smallest companions help them to hold the seeds, and eat in the same way. The ☿ feed the larvæ either by regurgitating the contents of their crop, or by directly presenting the aforesaid paste. According to Emery, Moggridge was mistaken in thinking that ants wait for the first signs of germination and chemical transformation of starch into sugar before eating their seeds. In denying this, he sums up his views as follows:

(1) "In artificial nests, the *Messor* heap up their seeds in the dryest chambers, and sometimes, but not always, carry them to the damp chambers when they wish to eat them; but they never leave them time to germinate. The germination of a few seeds in the granaries is accidental, and not the result of the ants' volition."

(2) "Seeds which have not begun to germinate are excellent food for ants. They make them into a paste or soup, which is certainly incapable of germinating."

(3) "The ants live on a paste which enters their crops and part of whose starch they assimilate; this is proved by quantitative chemical analysis of the paste itself, and of the remnants of ant-food when compared."

Emery has proved by a convincing experiment that *Messor* prefers the very germ of the seed to its pure fecula.

To put it briefly, *Messor* licks up and swallows a semi-liquid or semi-solid soup paste. Emery does not think that these ants deliberately dry their seeds in the sun, in spite of the positive observations of Moggridge, Neger and other conscientious authors on this subject. On the other hand, Cornetz wrote to tell him that in Algeria he had often seen thick tufts of wheat germinating, developed from the upper granaries of *Messor*, which retires further into the earth at the approach of winter. This confirms an observation by Moggridge, who once saw the seeds of a granary which had been abandoned by a *Messor* colony germinating in masses.

Escherich has observed *Messor* in Eritrea and confirms Moggridge's accounts. He adds that guards are stationed at the doors of every nest to examine each ant that arrives, before allowing her to enter. He also confirms the frequent errors committed by the ☿ in respect of the objects she gathers. On the Mediterranean coasts, *Messor* displays most zeal and strength in her harvesting during the day, especially about noon, whereas in Eritrea she works by night, after sunset. Here she also makes use of corn-chandlers' shops to rifle their seeds.

At Biskra, in Algeria, Escherich often brought away enough seeds from the granary of a single *Messor barbarus* nest to fill both his hands. In this connection he reminds us of the Talmudic rules of the Jews, which ordain in detail who is to possess the grains of wheat gathered from the granaries of ants—that is, which men are to possess them; for the Talmud takes no account of ants. If our Northern sages had studied the Talmud, they would not have denied the existence of ant-granaries!

Neger made some observations in the Island of Arbe, on the Dalmatian coast, where he saw *Messor* gathering seeds

from almost every plant growing on the island. Like Moggridge, he says that the sorting and cleaning of the seeds is carried on in the interior of the nest, as soon as the crop is brought in by the harvesters. Neger observed how damp seeds were dried in the air, and afterwards brought back to the nest by the *Messor* when perfectly dry; he also saw how these ants bite off the first shoots of the few seeds which germinate.

However, Neger does not believe, like Moggridge, that the *Messor* aim at transforming the starch into sugar by malting it. On removing the skin of seeds which have germinated somewhat prematurely, and examining them under the microscope, one finds that their endosperm (cellular protoplasm) is filled with starch-grains. This means that at the moment when the swelling of the seed causes the skin to fall off, if germination is prevented by the ants, the chemical transformation of the starch has scarcely begun. Here, therefore, Moggridge's interpretation seems to have been faulty, and Emery must be correct. Neger tends to think that the beginnings of germination help the ants to get rid of the skin of their seeds, which is often very hard.

Neger has also made the following very important observations with *barbarus*: Part of the material of the peeled and germinated seeds is worked up into masses of paste. At a certain moment a large number of these are taken out of the nest and laid out in the air to dry, like the damp seeds. They look very much like crumbs of black bread. Their size varies from that of a pin-head to that of a pepper-corn, and their colour is a light pink with a brownish tinge. When fresh these crumbs are damp and have a bitter taste, which more or less disappears by slow degrees when they remain in the air. The *Messor* leave them to dry until they are hard and crisp like a biscuit. In the morning Neger often saw the

a. *Zacryptocerus clypeatus* ♂. Brazil.

b. Do. do. ☿. Brazil.

c. Do. do. ♀. Brazil

d. *Harpagomya splendens* stealing honey-dew from *Cremastogaster* (*Physocrema*) *deformis* ☿. Java[2].

e. *Camponotus* (*Colobopsis*) *paradoxus* var. *janitor* ☿. Brazil.

f. Do. do. do. 2♀. Side view of head. Brazil.

g. Do. do. do. 2♀. Front view of head. Brazil.

h. *Machæromyrma bombycina* ☿. Algeria.

i. Do. do. 2♀. Front view of head. Algeria.

k. *Harpegnathus cruentatus* ☿. India.

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drying-ground covered with these crumbs of bread, but by the afternoon they had disappeared, though he had not seen the ants carry them back to the granary. Neger is convinced that the *Messor* use this ant-bread as a reserve-stock, and more particularly as food for the larvæ. Emery remains sceptical in this respect, and bases his opinions on his above-quoted observations as to the manner in which the *Messor* make and eat their paste.

The harvest-season varies according to climate. In the desert, the summer is the time of dearth, in the South of France the winter. Hence in France *Messor* does most of its harvesting in autumn, and in the deserts of Algeria and Tunis, in spring. The habits of one species sometimes vary according to habitat. Escherich found that in Algeria it is a regular thing for *Tetramorium cæspitum* to make fair-sized granaries; this ant is therefore a harvester in these regions and not in our own. However, in 1904, Escherich found a few granaries in some *T. cæspitum* nests at Strasbourg, just as I had found them in the case of *Lasius brunneus*, as quoted above, and as Emery and Janet had found in those of *L. niger*. Here once more, dear reader, when we look closely into things we see exceptions and transitions, and these are the very things that enable us to get in touch with the phylogeny of the harvesting instinct of certain genera such as *Messor*. I may add that the genus *Messor* crosses the Equator and flourishes anew in South Africa, where it even shows some forms very similar to *M. barbarus*.

Here I will refer the reader to Chapter VI of Part II, where I described the deep granaries of *Messor arenarius* reaching as far as a metre and a half down through the desert sand, and even farther down below the earth, like those of its relation, *M. Oertzeni*. The *Messor arenarius* tend

to go out singly to gather seeds, and the *Oertzeni* to form files of workers a fair distance away from one another. I have observed both of them harvesting in Algeria, Tunis and the Smyrna region during spring. The sand-craters of *M. arenarius* are semi-circular (see fig. 52 in Part II).

As we said at the beginning of this discussion, Sykes and Jerdon were the first naturalists to see *Pheidole* and *Solenopsis geminata* r. *rufa* harvesting in India. Sykes had even baptized one *Pheidole* by the name of *providens* (foreseeing), but no one can tell now which it was; I have also named one of them *Sykesi*.

In 1892 Wroughton described the harvesting habits of *Holcomyrmex scabriceps* of India. It marches in regular files on one or several well-beaten paths, cleared of all vegetation, starting from the nest-doors and travelling as far as 30 metres (as the files of our *Formica pratensis* do). When one of these paths crosses a bare rock, it shows up white against this rock. Wroughton supposed that this was due to chemical action (formic acid). *H. scabriceps* gathers and also deals with her seeds in the same way as *Messor*. Wroughton also described from Aitken's data the harvesting customs of *Pheidologeton diversus*, depicted in Plate III, *a*, *b*, and *c* of Volume I. Aitken saw about a dozen workers occupied in carrying one of the gathered seeds, the husks of which were afterwards thrown out of the nest on to the midden. He says that the communities are enormous; the medium-sized ☿ (*b*) sometimes lay a jaw to a burden, but the giants (*a*) appear to do nothing. Here Aitken is wrong; my readers have only to look at the worn-out condition of their mandibles as revealed in the illustration; they function as seed crushers. Armit, Tryon, etc., have observed the harvesting habits of *Meranoplus dimidiatus* and *Pheidole longiceps* in Australia. The latter deals with germinating seeds and dries those which

are wetted by rain exactly as does *Messor* in the account given by Moggridge.

Wheeler studied this matter in America, where he has distinguished as harvesters: *Solenopsis geminata*, twenty-two species of *Pheidole*, five of *Veromessor* and thirty of *Pogonomyrmex*.

Solenopsis geminata abounds in the American tropics, and stings formidably. The natives call it the fire ant, and it is highly versatile; it rears aphids, eats fruit, kills and devours many insects, and makes fine granaries containing very tidily-arranged seeds of tithymal and plantain. We have seen in Chapter IV of Part IV how it resists floods by forming live balls.

According to Wheeler, several harvesting *Pheidole* of America are incapable of preventing the germination of seeds and cannot bite off their first shoots. He thinks, like Heer, that the function of the ♃ is to cut up the prey brought home by the weak ☿ and enable the community to enjoy it. So, he says, they must do the same thing with the seeds. Hence they are at the same time butchers and bakers. Wheeler has seen ☿ feeding their larvæ directly with crushed seeds.

The fine *Veromessor* species inhabits the deserts and dry steppes of the Western United States. In appearance they are very similar to our European *Messor*, and have large ☿ with big heads, medium-size and small ☿. Their granaries are sometimes 60 centimetres below the hard soil of the sun-parched desert. Wheeler's description of their harvests, their granaries, their refuse-heaps, etc., corresponds exactly to the one Moggridge gives us of *M. barbarus* of Mentone.

Novomessor Cockerelli is a large, elongated and agile monomorphous ant, all its ☿ being of the same kind Wheeler tells us that instead of stinging they defend

themselves with the milk-white secretion of their anal glands. They carry one another about on their backs, like the *Leptothorax*. According to Wheeler, isolated *Novomessor* are omnivorous and also rodent, but they prefer fruit and seeds to animal food. In their refuse-chambers Wheeler saw the elytra of beetles and dried seeds, which he also saw some ☿ carrying. But he saw no granaries, and does not believe that they are fully developed harvesters like *Veromessor*. They bear more resemblance to *Aphænogaster*, which sometimes hunts, as *A. fulva* var. *picea* does in the United States and, according to Emery, *A. testaceo-pilosa* in Europe.

But the typical harvester of America is *Pogonomyrmex* of the deserts and steppes, with its psammophores. *P. badius* of Florida, which I myself found also in North Carolina, is the only one that inhabits cultivated ground. All the *Pogonomyrmex* of the United States make their nests in full sunlight. They are harvesters, and can endure long drought. Wheeler divides them into four groups:

1. The *subdentatus* group also includes three species of the sub-genus *Ephebomyrmex*. They are small, and their formicaries are scarce, the nests being small and scattered. The ☿ do not cut off the plants round their craters.

2. The *californicus* and *badius* group includes larger ants, one hundred to a thousand ☿ being attached to each colony. The craters are generally made in the sand, and the vegetation round them is not cut.

3. The *barbatus* group is the most famous, and possesses large species and very populous formicaries. *P. barbatus* cuts or rather saws off all the vegetation round its nest within a diameter of 1 or 2 metres. Beaten paths connect this clearing round the dome with the harvest-field. The nest is either nearly flat, as in the case of r. *rugosus* (fig. 88 in Part III) or built in a conical dome which may be 50 centimetres

high, as in the case of r. *molefaciens*, opening by a crater of pebbles. It has been claimed that this nest, with its granaries and galleries, may extend as deep as 5 metres underground.

4. The *occidentalis* group is distinguished by its enormous dome, an elegant gravel cone, represented in fig. 111. It is between 60 cm. and a metre in diameter and 20–30 cm. in height; and the nest underneath may reach to a depth of 3 metres. Around the dome all vegetation is cleared away over an area 2–5 metres in diameter. The opening is near the base of the dome. Fig. 111 is a vertical section showing the arrangement of the granaries and chambers.

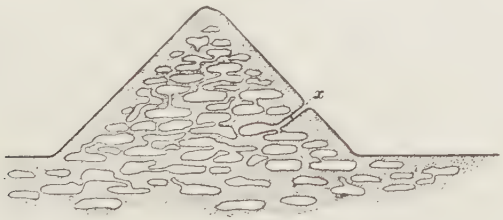

Fig. 111

Wheeler enclosed in an apparatus some small, timid, and inoffensive *P. imberbiculus* of Group 1, and watched them feed their larvæ with crushed seeds. Mrs. Mary Treat saw some *P. badius* of Group 2 not only picking up seeds but gathering them from their plants, carrying them up to the nest, husking them and depositing the chaff on the kitchen middens, and taking the seeds to their flat granaries. *P. badius* is the only polymorphic species, with large-headed ☿.

P. barbatus r. *molefaciens* of Texas was observed by Buckley, Lincecum and McCook under the name of the 'Agricultural ant.' In 1862 Lincecum claimed that *P. molefaciens*, not content with gathering seeds and storing them in her granaries, intentionally and exclusively

cultivated a species of grass, known as *Aristida oligantha*, all round her bare-domed nest and also sawed off, likewise intentionally, all the other plants growing within the circle, thus carrying out a well-devised agricultural system. Later on McCook wrote a large book entitled *The Agricultural Ant of Texas* (1879) in which, though he was not able to confirm the agriculture alleged by Lincecum, he did not dare to contradict it, and even produced plates depicting *P. molefaciens* domes surrounded by a narrow circle of *Aristida*. In this way he contributed largely to the spread of a myth which Wheeler tells us even the Texas schoolboy has come to regard as a joke.

Having lived for four years in Texas himself, Wheeler was the first to show these facts in their true light. The *Aristida* is very abundant and frequently gathered by *P. molefaciens:* its seeds may frequently sprout in the ant-granaries, which are literally stuffed with young plants. The ants may then be seen removing the seedlings which have sprouted too far to be fit for food, and throwing them on the refuse heap which is always at the periphery of the crater or cleared earthen disc. Here, however, the seeds often take root and form all round the dome the circle of *Aristida* drawn by McCook. As a matter of fact, other plants are found mingled with them, and it is only a minority of *P. molefaciens* nests which are thus encircled. The phenomenon in question is haphazard and irregular in its occurrence, and it was only the fertile imagination of Lincecum which transformed it into a general rule and created the legend of a calculated and exclusive cultivation of *Aristida*. This is the way, friend reader, in which legends are born in the human brain. Like undesirable weeds, they are easier to sow than to uproot, for in our stupidity we would fain have it so.

According to Wheeler, moreover, when *P. molefaciens* clears the grasses for some distance round its dome it is concerned to get the soil dried and warmed by the sun with a view to the development of the brood, as well as of its granaries. *Pogonomyrmex* coats her broken seeds with saliva before administering them to the brood, which "may insure the conversion of the starch into sugar," says Wheeler; so we see that interpretations differ, though facts remain. Wheeler has observed the nuptial flight of various *Pogonomyrmex* which never have more than one fertilized queen in their nest. The bite of *Pogonomyrmex* is terrible; I myself have felt that of *P. badius*. The ancient Mexicans made use of it to torture and kill their enemies.

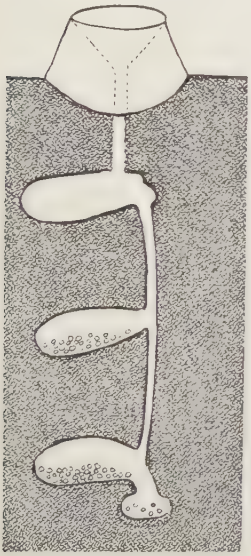

Fig. 112

Santschi observed the attractive granaries of *Oxyopomyrmex* in Tunis, as represented at half the natural size in fig. 112, drawn by Santschi himself. The upper chamber, which is built for the brood, is the only one without seeds. The nest is surmounted by a regular conical crater, and its opening is only 1 to 2 millimetres broad, just allowing one ☿ to pass through. The *O. Santschii* go harvesting singly. They are very slow, and at the slightest alarm they feign death or hurry back to their nest. The colonies consist of scarcely thirty individuals only. According to Saňtschi, *Oxyopomyrmex* has a very special kind of caustic poison. At Salonica I myself discovered *O. Krüperi* in a nest very similar to that shown in fig. 112. Fig. 113 shows the head of

O. Santschii, with its pointed eyes placed to the front and very low down.

Fig. 113

Prof. Lameere has made some fine observations in the Algerian Sahara. He saw some *Messor arenarius* nests still larger than the one which I myself excavated, and described above, and he calls this ant 'the most powerful organism in the desert.' He discovered *Messor caviceps* in a sandy desert where scarcely anything grows but drin (*Aristida pungens*). The cavity in the under side of the head of this *Messor* is specially devised to enable it to gather grains of sand which it has picked up with its psammophores. *M. denticornis*, found by Schulze in the Kalahari Desert (Namaland) and likewise a gatherer of *Aristida*, does the same, with its almost equally concave head.

Lameere also saw *Holcomyrmex Chobauti* and *Lameerei* (the second of which was discovered and described by myself) in the Sahara, gathering the drin-seeds, which are shaped like spindles and upon which the ☿ ride astride as the witches in the fairy-tales ride on their brooms. They bear them between their legs, holding the small end between their mandibles and fitting into the notches under their heads. These ants go harvesting in long files. Their nests open without craters by two or three orifices set rather wide apart and guarded by a few very timid ☿, which sham death by rolling themselves into balls when wind threatens to sweep them away. *H. Lameerei* lives in rocks, and *H. Chobauti* in pure sand, like *Messor caviceps* and *arenarius*. With regard to their local distribution, Lameere gives the following interesting table of the harvesting ants (*Messor* and

Holcomyrmex) and hunting ants (*Cataglyphis*) of the desert:

	OASIS	ALLUVIAL DESERT	STONY DESERT	SANDY DESERT
Harvesters:	*M. barbarus*	*M. ægyptiacus*	*M. striaticeps* *H. Lameerei*	*M. arenarius* *M. caviceps* *H. Chobauti*
Hunters:	*C. bicolor*	*C. albicans*	*C. viaticoides*	*C. bombycina* *C. Lucasi*

Edward Jacobson made a study in Java of *Pheidologeton diversus* already observed by Wroughton and Aitken and described above. The *Ph. diversus* march in long columns of workers, small and medium-sized, laden with seeds and prey, including even the fig-seeds contained in the excrement of certain birds. The giant ☿ or ♀ generally remain in the nest, where they crush the seeds, but when they come out they can be seen carrying small ☿ on their heads, as shown in Plate III of our first Volume. *Ph. diversus*, like *Formica pratensis* and *Holcomyrmex scabriceps*, hollows out beaten paths, 2–2·5 cm. broad, which the workers extend across the grass to a distance of as much as 50 metres from the nest, and on which they march both day and night. A certain fly named *Bengalia latro* watches for them and often flies down and snatches away their prey, with incredible speed, sometimes also carrying off some ants, of which it afterwards rids itself when it settles in another place. *Ph. diversus* is really omnivorous, and gathers almost as many live or dead creatures as seeds; and it is only the animal prey that is coveted by the fly, which discards the seeds when it takes them by mistake.

In Chapter III of Part IV I mentioned the wars of *Messor meridionalis*, observed at Braila in Roumania by my brother-in-law, Dr. A. Brauns. I append his important, if brief, observations on the habits of this ant.

"The *Messor* nest is built on a ridge 20 cm. high, with

holes on a level with the ground. During the rainy season these holes are closed to avoid flooding. Half-way up is a hole for the refuse. The holes are narrowed or entirely closed in the evening with grains of earth, and then opened again in the morning before sunrise. The giant ☿ do not work by day, but stay inside and act as policemen to the ♂ and ♀, which they drive out later on. In the winter I saw *Messor* throwing away their refuse (seed-coverings), almost exclusively on windy days and through the hole that was most exposed to the wind, so that it might be carried away immediately.

"April 22nd, 1918. Since October, 1917, we have had rain or dew on ten days only, but for the last two days warm rain has been falling. The *Messor* have been furiously at work, throwing out rubbish, digging their nest and surrounding their holes and craters. Between 5 and 6 p.m. I saw a little cluster some 30 cm. from a nest; a few giant *Messor* were struggling to drag a large individual out of the ground. This was a wingless ♀, which they were pulling by the body and legs. On looking about me I discovered three more apterous ♀ running about alone with a wearied air, apparently natives of several different nests, for they were 100–200 metres away from one another. I tried to put one of them into a hole in a nest near by, but she was attacked by a ♀ and fled. I repeated my attempts with the same results; the fertile ♀ was attacked every time by one or two of the larger ♀, which drove her away with her mandibles, but did not pursue her; she then fled of her own accord. One of these ♀, which I placed in a pot, endured the same fate next day.

"June 1st, 1918. The activity of *Messor* depends absolutely on the dampness of the weather; as soon as rain has fallen, it begins to dig and toil both day and night, whereas *Cataglyphis* only works by day.

"August 9th, 1918. For a long time all has been as still as death, and the *Messor* nests have been entirely closed. To-day, after a few rain-storms, a hole 30 mm. wide was opened, and ☿ of all sizes set out to gather thistle-seeds."

What were the *Messor* about when they drove their fertile ♀ away after this exceptionally dry year? I leave it to the future to elucidate this problem, which at present is inexplicable.

In 1920 Prof. Franz Doflein published in his *Mazedonische Ameisen* the interesting observations which he made in Macedonia in 1918. For the most part these researches concern the same *Messor meridionalis* which Dr. Brauns observed at Braila, but this time they relate to a mountainous country (Uskub, Kalukova). Passing over his confirmation of the previous work, we will summarize the following aspects of his study:

In December and January it was freezing, and the *Messor* slept, without eating anything. They came out to work for a few days in February, then, their home being in the high region of North Macedonia, they went to sleep again. Doflein attaches considerable importance to what he calls the 'collecting instinct' which urges *Messor* to gather not only seeds, but all kinds of useless objects, which are afterwards thrown away (Moggridge's 'mistakes'). Summer is the gathering season for *Messor* in Macedonia; they then gradually dig and clean a number of paths 30–100 metres long, and their formicaries frequently form polycalic colonies, with nests the same distance apart.

He insists that all the ☿ of different sizes may participate in this work. He admits, however, that the pygmies and giants take a smaller share in the gathering of seeds than the ☿ of medium size. He describes the harvests, the nests, etc., in a detailed manner which is quite delightful, helping out

his statements by the use of figures. He cites one nest which contained thirty granaries and a whole litre of seeds. These nests were built in earth, so hard that after a whole day's rain the moisture had not sunk further than 3 centimetres into the ground. The *Messor* nests are not usually very deep; at times, however, they may extend a metre or even one and a half metres down. Doflein destroyed them with the help of a Roumanian.

In his observations on *Messor meridionalis* in an artificial Fielde nest, Doflein declares that he discovered the origin of the cement of mica and flint described by Moggridge. It is a whitish substance similar to wax, and it helps to secure the granary walls from the damp. He saw the glass walls of a Fielde nest gradually covered with light grey filaments, 3–6 millimetres long and beginning from a large base about a millimetre wide. He then observed the same thing happening on the walls of natural nests. These filaments, illustrated in Doflein's book, are not soluble in water, but can be easily wiped off the glass. Though he was not able to observe distinctly the way in which *Messor* produces this putty-like material, produced in darkness, especially when the Fielde nest had been exposed to the sun, he says that the ants probably apply the cloaca, and perhaps the mouth also, to the glass, and spread over it the secretion of a gland (the anal, accessory, mandibular, or some other gland); and then, as they walk about, leave this glutinous secretion which forms the filaments in question. He sometimes thought he could see some scraps of excrement near the base of the filament. He thinks that the *Messor* adopt this means of keeping their seeds dry to prevent them from germinating.

Doflein saw the *Messor* arrange their seeds neatly in order. He never observed the ants eating them or putting them

out in the sun, but he often saw the seeds being borne to a damp place, where, on one occasion, they germinated and grew up into plants. Doflein does not entirely reject Moggridge's theory, according to which the seeds are transformed into malt before they are eaten. This, he says, may or may not happen according to the circumstances, species and region. Doflein did not observe the loaves made out of paste, which Neger describes and which we have mentioned above. In short, he confirms Emery's opinions, but he believes that in Macedonia the *Messor* are chiefly insectivorous, and that the seeds are used as a special reserve for the time of want and as food for the young.

Doflein also discovered *M. Oertzeni* in Macedonia. He furthermore observed the polyandrous nuptial flight of *M. meridionalis* ♀. This flight is not a high one, and mating takes place in the neighbourhood of the nests; the couple can then often be seen falling to the ground, as in the case of *Myrmica*. The ♂ die shortly afterwards.

He once saw a giant ☿ caress with her antennæ a pygmy ☿ which was all tangled up in some wadding, then pull her in a friendly way, free her, and finally leave her alone.

He next observed *Pheidole pallidula*. He declares that their ☿ disgorge honey-dew to the ♃, but that the reverse never takes place. What is more, when all the ♃ in a Fielde nest managed to escape through a little rift, and did not return, for a reason unknown to our author, the ☿ and the fertile ♀ remained there alone, as their heads could not pass through the rift. The result was that they starved to death, without touching the honey which Doflein gave them. This important observation must be carefully confirmed. As Doflein says, it presents a strong contrast to the case of *Messor*, whose ☿ polymorphic forms, so he declares, all

possess an equal capacity for work, particularly for feeding their companions.

There, then, all things considered, we have some examples of important divergences between various authors concerning the harvesting ants, and especially as regards their interpretations of observed facts. You must get to work, therefore, friend reader, and correct and complete all this, for there is no shortage of subject matter.

Thus I end my present chapter to go harvesting elsewhere, namely, in the fungus-gardens of the *Attini*.

Chapter III

MUSHROOM-GROWING ANTS

Ever since tropical America was discovered we have known that it is inhabited by certain ants which the Indians called 'Sauba,' and which are in the habit of devastating plantations by cutting off leaves from trees with their strong sharp mandibles. They may be seen journeying in long files, one or two rows deep, laden with leaves which are still green and which they have just cut off; or climbing on a tree or a bush, as depicted in a most faithful manner in figs. 114 *A* and *B*, especially *B*, which were carefully drawn by Heinrich from nature. Everybody in these parts has seen it. What the Sauba do with their leaves nobody knew at all until 1874.

They were seen going into their subterranean nests with their cut leaves, but there the leaves were seen no longer and the most absurd conjectures were current. I do not know whether the Indians or the Creoles were the first to spread the story that the Sauba cut leaves simply as carpets for their nests; but Bates, who so well described the habits of *Eciton* (Chapter I), was himself responsible for a similar tale in 1863. He claimed that he had seen some *Atta cephalotes* carpeting their nest with the leaves they brought home, covering them with earth in order, so he thinks, to keep out floods. His imagination led him into error. One night, moreover, the *Atta* stole the manioc seeds which he had

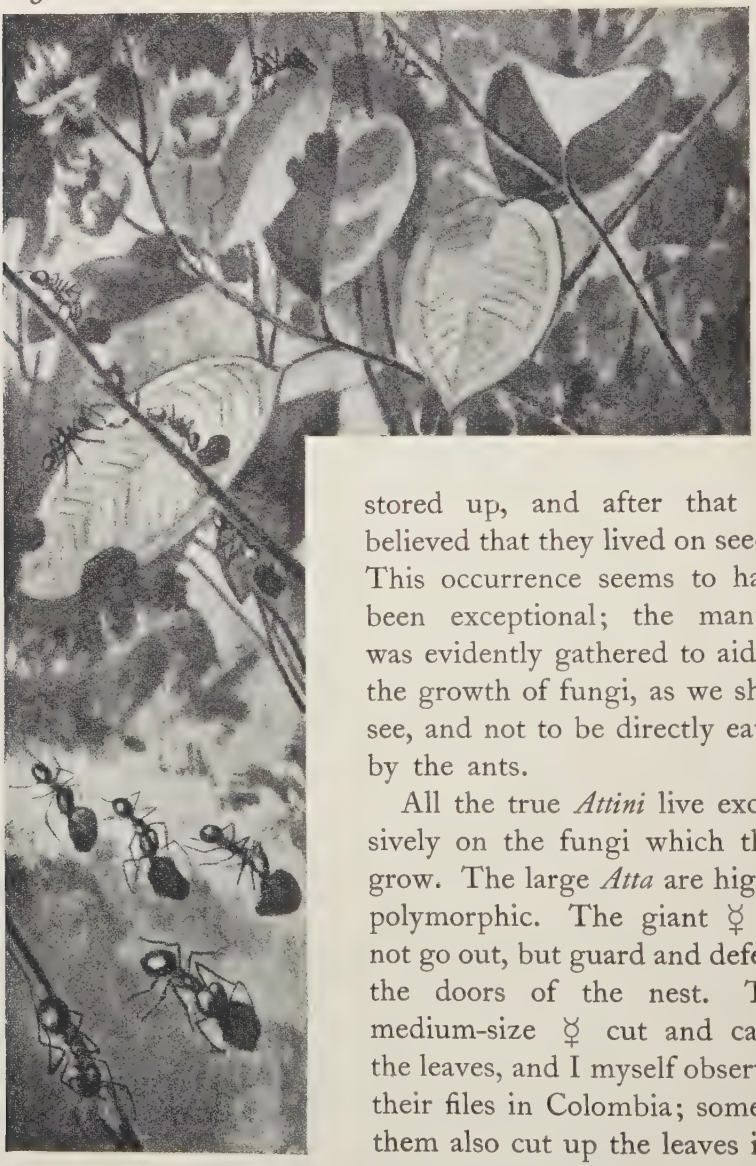

Fig. 114 A

stored up, and after that he believed that they lived on seeds. This occurrence seems to have been exceptional; the manioc was evidently gathered to aid in the growth of fungi, as we shall see, and not to be directly eaten by the ants.

All the true *Attini* live exclusively on the fungi which they grow. The large *Atta* are highly polymorphic. The giant ☿ do not go out, but guard and defend the doors of the nest. The medium-size ☿ cut and carry the leaves, and I myself observed their files in Colombia; some of them also cut up the leaves into little pieces within the nests, as Möller proved. The Lilliputians do not leave the nest, but sow the fungus-spores, cut the filaments of mould and keep

the fungus-garden clean. In the ☿ of *Acromyrmex*, dimorphism is already much slighter. Finally *Trachymyrmex*, *Apterostigma*, *Mycocepurus*, *Myrmicocrypta*, *Cyphomyrmex*, *Sericomyrmex*, etc., have monomorphic ☿, all identical with one another. The *Attini* which are peculiar to tropical America, as we saw in Part I, Chapters I and VI, are descended by a long phylogeny from small ants of the Old Continent, relations of the smallest American genera. There are no ants outside America which grow fungi.

Fig. 114 B

Belt was the first to discover the truth while in Nicaragua in 1874, and he revealed it in the book quoted above. In this region he was often told that it was no use attempting to grow such and such a plant because the Sauba always destroyed it. When an *Atta* has partially cut through a leaf on a tree, it looks as if she is going to fall, but as a rule, so Bates tells us, she holds on to the rest of the leaf by a leg and thus raises herself, carefully arranges the cut portion of the leaf between her mandibles, carries it down from the tree and follows the column formed by her companions as they return. This column is often about 15 centimetres or more in width. When an *Atta* does fall, however, she will not relinquish her leaf for such a trifle, but picks herself up and carries it away. The nests of the large *Atta* are not built in the undergrowth of the virgin forests, but on its outskirts or round clearings.

On reaching their nest, says Belt, the *Atta* make

their way in with their green leaves through the large openings, and disappear, covering up with their mass of leaves the ☿ which are coming out and crossing their path. Through other nest-openings, still more ☿ can be seen coming out with balls, which Belt supposes are made of earth, and which they throw out to raise their dome higher and higher. He wondered how the forests remain proof against these ravages, but the strength of the tropical vegetation enables them to do so none the less. In Colombia in 1896 I confirmed Belt's observations, word for word, with *A. columbica* in particular, but also with *A. lævigata* and *cephalotes*. It is not earth, however, that is thrown out by the ☿; usually, at any rate, these balls consist chiefly of the inedible refuse of the fungus-gardens, as I had opportunity to observe in Colombia. It is chiefly imported plants which are destroyed by the *Atta*. On the whole the indigenous vegetation, gradually reinforced by natural selection, resists the attacks of the Sauba ants.

By flooding their galleries with phenic acid, Belt succeeded in discouraging the ants which were devastating the trees in his garden, and he watched them hurry away and remove their belongings to another nest farther off. The *Atta* carried out the numerous corpses of their companions which had been slain by the acid, and bore their brood and their fungus-gardens, cut up in pieces, to the new nest. On reaching the top of a steep slope they were intelligent enough to let go of the pieces and allow them to roll to the bottom, where other ☿ picked them up and carried them to the new nest. As Belt remarks, this shows an extraordinary reasoning capacity. A few days later both the nests were empty. The *Atta* had removed to a still more distant spot. The garden was not invaded again for a year, and then Belt again drove the *Atta* away in the same manner. The

underground ramifications of the nests of these ants are so deep and extensive that energetic steps are required to save oneself from their ravages.

Another method pointed out to Belt by Fr. Velasquez is to use corrosive sublimate, as I have already explained in Chapter V, Part II, when describing my own experiments with *Myrmica*, which repeated those of Belt with *Atta*. But if the sublimate is used in dry weather, the effect on *Atta* seems to be much more intense. Under the action of this poison, individuals of the same formicary cut each other to pieces and mutually destroy one another.

Belt was the first to realize that the *Atta* utilize their leaves by cutting them into small pieces on which grows the mycelium (mould) of a fungus which they use as food. They are, he tells us, 'mushroom growers and eaters.' To destroy them he dug down deeply into their nests, and there he discovered rounded chambers as large as a man's head, communicating with each other by broad passages, like those shown in figs. 115 and 127, photographed from life. Although the ☿ were continually carrying in cut leaves, no quantity of them was ever found in any part of the burrows. Hence it was certain that they must be immediately worked upon and used up in some unknown way. The chambers were always filled with a spongy mass, speckled, brown, light and loosely connected. Throughout these masses were scattered the larvæ, pupæ and smallest ☿ of the *Atta*. The masses themselves were composed of small fragments of leaves, withered to a brown shade and connected by filaments of a mycelium fungus. Belt found the same cavities and the same spongy masses, serving at the same time as food and nest for the brood, with another species of *Atta*. In the night, this species often enters houses and steals farinaceous substances, as they stole Bates' grains of manioc.

Belt adds that the *Atta* are not content with leaves, but will take anything that may serve for growing their fungus on: the white rind of oranges, various flowers, etc. Belt says that the *Atta* neither dry nor moisten their leaves; during the rains they bring them into the nest and during the dry season they go out at night to cut them.

Belt supposed that the smallest ☿ comminute the leaves, as he never saw them being either cut off or carried outside the nest by the small ants or the giant ☿ which guard the doors. Here Möller has proved him to be wrong. These large creatures defend the formicary and go out only when a removal takes place; they bit Belt so severely as to draw blood. It is the mediæ which act as bearers outside the nest, and which also cut up the leaves inside.

Here again the observations which I made with the large *Atta* of Colombia in 1896 confirm those of Belt. While spending a night near Rio Frio, on the farm of Mr. Bradbury, I found an enormous *Atta columbica* nest, the centre of a large polycalic colony, the inhabitants of whose various nests were on friendly terms with each other. A number of roads, a decimetre broad and as well cleared as those of our European *Formica rufa*, radiated from the central nest, and over these ran thousands of *Atta* ☿ carrying cut leaves. The central nest itself was 5–6 metres in diameter and 1 metre in height. It was like a miniature volcano, consisting of twelve to twenty volcanoes set close to one another. The largest was 60 cm. broad by 28 deep, and continued below through a passage $3\frac{1}{2}$ cm. broad, into which poured masses of ☿ returning to the nest laden with cut leaves. The other dwellings, which we will call the accessory nests, were situated one or two hundred paces away from the central nest; they were much smaller and had only two or three craters.

There are two kinds of craters: one grey, built out of earth or sand, which is excavated when the nest itself is being made; the other brown, and merely the outcome of refuse from the fungus-gardens, which is inedible, since all the nutriment has been extracted from it. From this second type of crater numbers of medium-sized ☿ may be seen coming out, laden with large brown pellets, which they immediately throw out all round the summit, only to take them back into the nest soon after. This sight, contrasted with that of the ☿ laden with their green leaves and hurrying in through the grey craters, made an indelible impression on me, and was somewhat suggestive of a factory with its workmen.

Having made up my mind to see the inside of the nest, I asked one of Mr. Bradbury's Indian servants, who had a spade, to make a large breach in the central nest of the *A. columbica*. No sooner had he thrust in his spade two or three times and laid the nest open over a surface of about a metre, than the *Atta* crowd, which had hitherto been quite peaceful, rushed furiously towards us. The Indian threw down his spade and fled. In a few seconds I was covered with *Atta*, which drew blood from my hands, face and calves, and I was compelled to retire, followed by a host of large ☿, until I was several metres from the nest. They must have seen me, for they pursued me in a straight line wherever I turned to escape from them. I then returned for a moment, fastened down the bottoms of my trouser-legs, donned gloves and a scarf and went back to the fray armed also with a cigar-box. There in front of my eyes were about twenty large chambers (see fig. 115), each 15–20 cm. broad with the fungus-gardens and brood of the *Atta*. I filled my cigar-box and fled again, covered with the desperate defenders of the nest. The large *Atta* bit my skin and drew blood, even cutting a

small artery in my finger. I measured other cuts 3–4 millimetres long on my fingers and in other places. The *Atta* ran very swiftly with their long legs (fig. 114*B*), and in less than no time they had climbed up my clothes and reached my face.

The fungus-gardens I captured were of a light reddish colour near their base, with spots of white mould, the top being more of a grey tint. The dark portions seemed to be

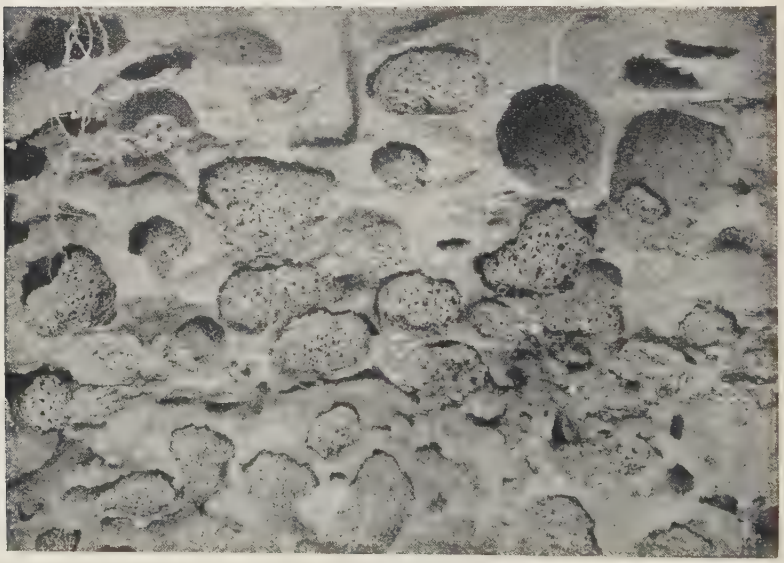

Fig. 115

waste-products. In the labyrinth formed by this fungus-culture were thousands of minims mingled with mediæ, not to mention the brood. Some enormous ♀ larvæ lay there, covered with the Lilliputian ☿ until they looked like hedgehogs. They held on so fast that I was able to put them and the big larvæ into alcohol as they stood, and presently to show this hedgehog to my colleagues at a congress. But the

fungus-garden is so spongy and flocculent that it crumbles at the least pressure, and cannot be preserved whole. I have kept the remains of it, however, and on examining it under a microscope in 1921, after 25 years, I was able to affirm that it contained: (1) A great many small fragments cut off from leaves, brown in colour and about 1 or 2 millimetres or even less in length (these fragments were covered over with the mycelium fungus and tangled with one another); (2) small clusters of 'kohlrabi,' identical with those represented in fig. 117*A* (see below) after Möller. These kohlrabi are microscopic, invisible to the naked eye, or nearly so. To my shame I admit that I neglected to make this examination for 25 years, as I was relying on the work of Möller.

When I had got rid of the *Atta*, I presently opened the cigar-box. As the ants were no longer there, the mycelium fungus had grown and the whole box was filled with a mould, whose long filaments were beautifully white. I then sent the box to Möller, who used it to prove that the fungus cultivated by the large *Atta* is the same as that of *Acromyrmex*, which he alone had observed—namely, *Rhozites gongylophora!* I never saw any trace of carpets made out of leaves in the *Atta* nests or in those of the *Attini* in general. This myth is exploded. In Colombia, on the other hand, I observed that the *Atta* do not carry companions which have lost their way on their backs, like *Myrmica*, *Tetramorium*, etc., but folded up underneath them, like *Formica*.

The nests of *Atta lævigata* are very large, but quite flat and subterranean, and therefore I never succeeded in digging deep enough to find their fungus-gardens. *A. lævigata* lives on mountains at an altitude of about 1,000 metres. The same obtains with *A. cephalotes*, whose nests are intermediate in style between those of *lævigata* and of *columbica*, though its gardens resemble those of the latter species. The giant ☿,

which in *columbica* sometimes come out of the nest, are never seen outside in the case of *lævigata* and *cephalotes*, but are therefore all the better door-defenders, and terrible biters. In *lævigata* they are enormous, while the smallest kind are truly Lilliputian, being only 2 millimetres long, whereas the giants are 16 millimetres long, and the ♀ 23. The heads of the giants, however, are 6 millimetres broad across the occiput. Between these are all possible intermediate sizes. From the above data, dear reader, you will be able to realize what the large *Atta* are like; to complete the image, add that they have a reddish colour and their bodies are covered with spines (fig. 114*B*).

But we have still to consider how the mycelium of the mould is transformed into microscopic kohlrabi, what is the mysterious fungus of the *Attini*, and by what means its mycelium is cut off and its reproductory corpuscles are sown —the microscopic cells known as 'spores', from which all fungi are derived. All fungi, the largest agarics as well as the boletus, come from microscopic spores, which begin in the form of mycelium, otherwise known as mould. Only occasionally do these moulds suddenly give rise to the various species of large mushrooms which are familiar to all of us, and whose non-poisonous species are so delightful to eat. But to distinguish one mycelium from another, it is necessary to be a botanist and to be able to recognize them under the microscope. Neither Bates, nor Belt, nor myself have specialized in this subject.

Acromyrmex. We are indebted to Dr. Alfred Möller, a distinguished botanist who afterwards devoted himself to forestry and became a professor, for the most exhaustive study of the *Attini* and their fungus-gardens. This study was made in 1893 at Sta. Catharina in Southern Brazil, and dealt especially with *Acromyrmex*, but not with the large

Atta. He then wrote to me, and I identified his ants. He quotes Belt at great length, and even takes Belt's remark: 'The *Attini* are mushroom-growers and eaters' as the motto of his admirable work. Here we will summarize Möller's book, *Die Pilzgärten einiger südamerikanischer Ameisen* (The Fungus-gardens of certain South American Ants). Möller describes the habits of four species of *Acromyrmex: A. disciger* Mayr, *A. niger* Sm. (which I then distinguished wrongly as *hystrix* Latr; it has been found out since then that the true *hystrix* is a synonym of *octospinosus* Reich, and lives farther north), *A. subterraneus* For. (which I, again, confused with *coronatus* F., and which was thus named by Möller) and *A. Mölleri* For. (Möller's *Atta* IV).

These four species dig and build roads in the grass like those of the European *Formica pratensis*, 1·5 cm. broad and sometimes covered with earth-masonry, like those of our *Lasius niger*, and along them, single files of *Acromyrmex* ☿, laden with cut leaves, march one behind the other. Other squads repair and reconstruct the road, which is frequently destroyed by various creatures. When this happens, the ☿ which are stopped by the unforeseen obstacle often lay down their leaves, picking them up again as soon as the repairs are finished. Möller saw an *A. disciger* take an hour and ten minutes to carry a leaf twice her weight a distance of 26 metres. But outside beaten paths of this kind—in the forest, for example,—Möller saw some *Acromyrmex* ☿ cut off leaves more than 20 metres up a tree, carry them down over the leaf of a large fern, cross over the lianas, come to the ground and rejoin their companions on the road. In this way the *Acromyrmex* sometimes make a road 100 metres long, or longer, utilizing branches and anything that can aid in their passage, even for the purpose of carrying them over streams, and bearing their leaves the while.

These means of passage often alternate with open or covered roads. From time to time a shower will cause the *Acromyrmex* to throw down their leaves suddenly. I may add that *A. niger* cuts its leaves by night.

Möller observed through a lens the way in which the *Acromyrmex* cut leaves with their dentated mandibles, which

Fig. 116

they cross like a pair of scissors. Either can be placed over or under the other. They always make cuts on the leaf in the form of an arc or circle. When a vein has to be cut through it must be gnawed several times. The size of the piece cut depends on that of the ant. Möller has seen a leaf cut right through in four or five minutes, after which the

carver, still attached by one or two legs to the uncut part, proceeded like the *Atta* in Belt's account above. The burdens of the ☿ render it difficult for them to move about, and therefore they generally carry their leaves on their backs, to obtain greater freedom of movement. They also gather berries, flower-buds, etc., as manure for their fungi.

A. subterraneus forms its nest of masonry in the earth. The three other species simply cover their homes with dry leaves and twigs, somewhat in the manner of *Formica rufa*, as shown in fig. 116 (*A. Lundi*) after Dr. Bruch; but the dome of the nest may be either uncovered or else covered to a variable extent. In no case does the fungus-garden touch the lateral and upper walls of the chamber in which it is formed, as is made evident by our figure, and it was not left uncovered by any of the four species observed by Möller, any more than by *A. Lundi*. *A. octospinosus* of Para and Colombia is different in this respect. *A. subterraneus* was the only species observed by Möller which had several fungus-gardens, buried in the earth and enclosed in chambers connected by passages. Except in the case of *A. Mölleri*, in which they are only 3 cm. broad owing to the smallness of the community, these gardens are almost as large as a human head.

Near the top, where it is still fresh, the garden is blackish-blue in colour. Lower down, where it is old, it becomes reddish-yellow. When it is destroyed, the ☿ gather up the blue-black part first of all. The filaments of mycelium (mould) link together certain small, round, white bodies about a quarter of a millimetre in diameter. These are the 'kohlrabi,' the sole food of the *Attini*, represented in fig. 117*A* in connection with *Acromyrmex* and *Atta*. Under the microscope they show small remains of finely-cut leaves, threads of mycelium anastomosed (connected) with each

other, only 5–6 myriametres thick. At the ends of the filaments of certain mycelia are globular kohlrabi measuring 10–24 myriametres across, that is, about 1/10–1/4 of a millimetre. There are transitions between the kohlrabi and the threads of mycelium, but quite apart from any of its dilations the mycelium proliferates throughout the entire fungus-garden.

Möller took a garden from an *A. disciger* formicary and spread it over a path a few metres from the nest. In three-quarters of an hour the ☿ had found their nest again and carried the whole garden back to it in pieces. If it is destroyed they promptly restore it and cover it over afresh with dry leaves and other fragments. When they migrate they take it with them, leaving intact the shell of the nest they are abandoning. In short, the *Acromyrmex* are inseparable from their fungus-gardens.

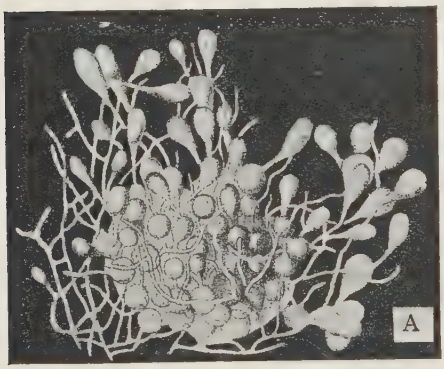

Fig. 117 A

These ants are much smaller than the *Atta*, and incapable of drawing blood from the human skin. They will starve to death beside their leaves, which they cannot eat, but will protect their gardens from all dangers, even including light, and when deprived of them they perish. They utilize the refuse of the ant-gardens to make the outer framework of the nest which is to cover it. In order to see them eat, Möller starved his *Acromyrmex* for five days and then gave them some kohlrabi, watching them through the magnifying

glass. A ☿ seized a single kohlrabi head with her mandibles, tore it from the garden, placed it between her forelegs, sucked and then swallowed it, turning it round several times in her mouth and probing it the while with her antennæ. After Möller had starved four species of *Acromyrmex* for a long time, he saw each of them eat the kohlrabi of the other species in the same way, though they would never touch those of *Apterostigma* or *Cyphomyrmex*.

On reaching her nest, *Acromyrmex* first cuts a leaf in two, then divides one of the halves and so on. As soon as one of the pieces becomes small enough the ant turns it round and round between her front legs and mandibles, examining its shape as she does so, and then continues to slice it up until it is about as large as the head of an *Acromyrmex*. Every worker cuts her leaves in the same way. She proceeds to take her fragment between her front legs, places the edge between her mandibles and pinches it all round without cutting it, as the magnifying-glass clearly reveals, after which she scratches the fragment until the surface is all peeled off and the whole is softened. With these same mandibles of hers she then makes a pellet of paste, an operation which may occupy her for a quarter of an hour, takes it to some site suitable for a fungus-garden, and lays it in place with her head and front legs, like a mason handling mortar. As she does this, she continually probes the pellet with her antennæ. In a few hours, the mycelium of the fungus finds its way into this new manure, which has been so carefully prepared ; and by the afternoon it has already covered the pellets of triturated leaves which were formed and set in place that morning.

Möller succeeded in making an admirable observation of *A. Mölleri* carrying out its whole routine, while fully exposed to the daylight, in a basin which he had surrounded

with petrol in order to hold his ants captive. This also enabled him to be an eye-witness of the formation of a fungus-garden, similar to that represented in fig. 120. In spite of Belt, it was always the mediæ and not the smallest ☿ which Möller saw skinning and compressing the leaves and constructing the garden with them. The pygmies were unable to do this, their mandibles being too short; they lie hidden in the smallest cavities of the fungus-garden doing something quite different; what that is we shall see shortly.

On removing all the ants from a very neat fungus-garden Möller saw the mycelium of *Acromyrmex* grow within 24 hours outside the garden, its filaments attaining a length of 2 cm. in two days. While in Colombia in 1896, I made the same observations with my *Atta columbica* in the cigar-box—as we saw above. The kohlrabi then disappeared, being absorbed by the mycelium, whose filaments then produced cellular swellings of their own, known as conidia, which are peculiar to fungi in the natural state and are also characteristic for each species. The conidia must therefore not be confused with the kohlrabi, which are the product of an artificial culture by the ants, in spite of the apparent resemblance which is frequently noticed between these two kinds of swellings. Möller spent two years growing *Acromyrmex* fungus-gardens according to Brefeld's method, that is, by means of appropriate cultures.

Whenever some mistake enabled a few pygmy ☿ to remain alive in Möller's artificial fungus-garden he saw them working to prevent the mycelium from growing; they cut off its filaments, and re-established their kohlrabi garden as far as possible. But when they are too few, they have to flee before the growing mould, carrying the larvæ they wish to save. Hence they flee from their own work, which threatens to suffocate them. Even when about

twenty pygmy ☿ succeed in preventing this suffocation occasioned by the presence of the mycelium, their frantic toil does not enable them to remove the spores from all the ordinary strange fungi, as they did to begin with, for these spores in their turn now invade the garden of *Rhozites*, in other words, its kohlrabi, and destroy the whole structure.

Möller succeeded on his own account in inducing the

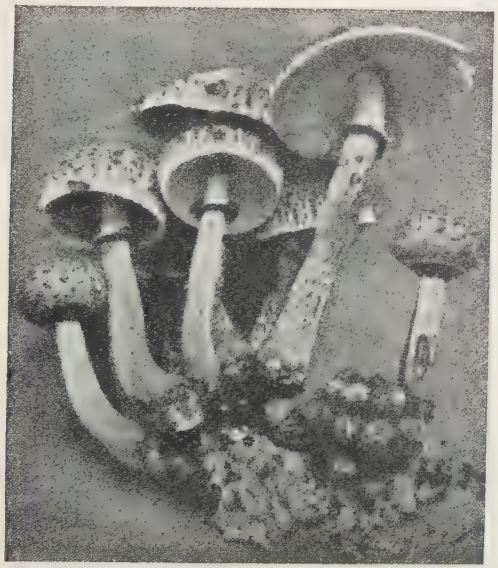

Fig. 118

kohlrabi to reproduce their species simply by growing them, without their mycelium, in his culture. They were not transformed into conidia. In a word, the kohlrabi are the product of an artificial culture of *Rhozites gongylophora* by *Acromyrmex* and *Atta*. As soon as the gardeners are removed, their gardens are transformed into ordinary mycelium, with conidia, etc.

With the help of a friend, Möller succeeded in discovering, on four occasions, the definite adult form of the large fungus of *Acromyrmex*, *Rhozites gongylophora* Möller, represented at only one-fourth of the natural size in fig. 118, taken from his own illustration. It is wine-red in colour, 16–20 cm. high, with a cap which may attain a diameter of 16 cm. It is an agaric belonging to the family of *Amanita* or *Lepiota*, and resembles *A. melleus* and *squarrosus*, with its scaly cap, which we eat in Switzerland. On each of these occasions it was planted in the milieu of the ants' fungus-gardens. But this was not enough; it was necessary to prove that the kohlrabi of the ants was indeed the product of its mycelium. Möller first showed that the malt-like odour of the full-grown fungus is identical with that of the miniature kohlrabi. Again, the *Acromyrmex* fungus-garden immediately adhered every time to the base of the large mushroom-stems, as shown in fig. 118. Above all, Möller succeeded in growing kohlrabi in his culture from spores carefully chosen from the very cap of an adult *Rhozites* or one of its fragments. All kohlrabi of this kind were eagerly devoured by *Acromyrmex disciger*, *niger* and *subterranneus*. Möller also succeeded in making his *Acromyrmex* eat the *Rhozites* cap itself in very small fragments, which they snatched up as he watched them. Finally, he managed to cultivate conidia, etc., identical with those growing on the mycelium, on a fragment of the base of the adult *Rhozites* which he took away. In short, no shadow of doubt remains as to the specific identity of the various forms of *Rhozites*: mycelium, conidia, kohlrabi and large adult fungus.

Möller tells us that countless different kinds of leaves are cut by *Acromyrmex*. Nearly all plants yield them their tribute, though very rarely, it is true, in some cases. Generally, though not always, it is the plants cultivated by man which

suffer most. The leaves of a few imported plants, such as celery and gourds, are rarely cut, whereas *Acromyrmex* is very fond of certain indigenous plants. Grasses are nearly always spared. Maize-seeds, however, are sometimes stolen and utilized as manure for the kohlrabi.

Fig. 119

Apterostigma. Möller also studied the fungus-gardens of four species of this genus belonging to the *Attini: A. pilosum*, *A. Wasmanni*, *A. Mölleri* and *A. Mayri* v. *discrepans*, the last of which he calls *A.*IV, for in 1893 I had not yet determined its identity. The fungus-gardens of *Apterostigma* were

discovered by Anna Brackes. These ants are to be found in old tree-trunks, and build their fungus-gardens from fibres of decayed wood, caterpillar excrement, manioc-flour, etc. All the *Apterostigma* grow the same fungus, but *A. Was-*

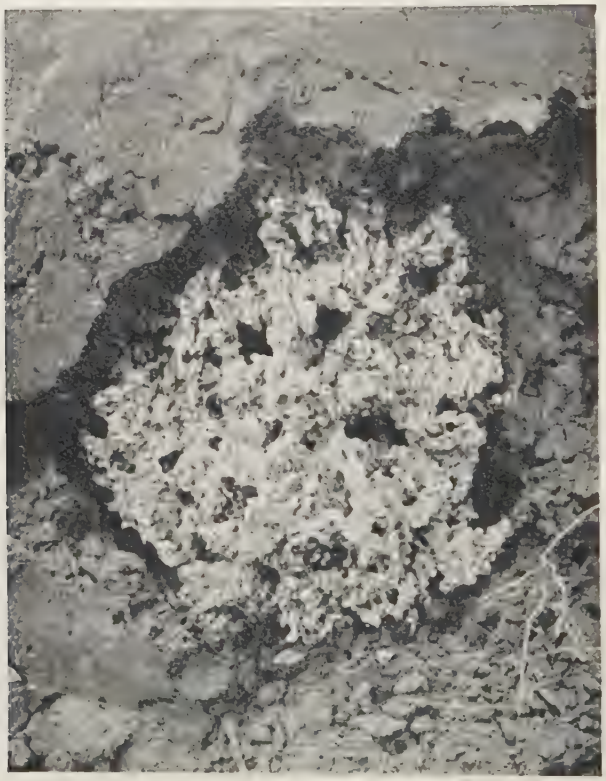

Fig. 120

manni has carried the culture of this species much farther than the others by constructing distinct, separate heaps of kohlrabi, which are less perfect, however, than those of *Acromyrmex*. Fig. 119 represents the Argentine *Apterostigma*

Bruchi itself, and fig. 120 its fungus-garden, from a photograph by Dr. Bruch.

A. pilosum lives in small colonies of 12–20 ants. It is very timid, and feigns death for a much longer time than the other species. Its fungus-gardens are hung in some crack in a decayed trunk, and surrounded by a protective sac which constitutes the entire nest and appears to be woven. This sac is only 3 or 4 centimetres in diameter; in reality, it consists of mycelial filaments, specially worked into shape after being pressed and cut off from the mycelium by the ants. Is it not surprising, dear reader, that ants should weave their sacs sometimes with the mycelium of a fungus and sometimes with the thread of their own larvæ, utilized as shuttles, as we shall see in the next chapter. Möller's observations on the construction of the fungus-garden and its sac were made with some captive *A. pilosum*. He watched these ants eating their own kohlrabi, which are very imperfect, as well as those of the other species of *Apterostigma*, just as the various species of *Acromyrmex* borrow from one another. On the other hand, even after a long fast they disdained the kohlrabi of *Acromyrmex* and *Cyphomyrmex*.

In a word, therefore, the *Apterostigma* do not cut leaves and do not march in line. They bear their burdens between their legs, not on their heads. Their ☿ are all nearly equal in size and show no polymorphism. Their kohlrabi differ from the mycelium less than those of *Acromyrmex*, and are no longer in shape. By removing the ants Möller succeeded in this case also in growing the mycelium and its conidia, which are very different from those of the *Rhozites*. Hence it is clear that the *Apterostigma* also cut mycelium-threads in order to grow their kohlrabi. Möller did not give a name to the *Apterostigma* fungus, whose definitive adult form he had

no opportunity of seeing, but, he says, everything points to the assumption that it is a member of the Agaric family like the *Rhozites*.

Cyphomyrmex. This is a genus of small *Attini*, one species of which, *C. Wheeleri*, is represented in fig. 122. Möller studied *C. strigatus* and *auritus*. Their fungus-gardens are neither suspended nor constructed in a sac, but are found in the same places and built in the same way as those of *Apterostigma*. Möller saw some belonging to *C. strigatus* which were 8 cm. in diameter, and some belonging to *C. auritus* which were 15. They grow on wood, caterpillar-excrement, etc., like those of *Apterostigma*. The two species cultivate the same fungus, which is, again, quite a different species from those of *Apterostigma* and *Acromyrmex*. But, here too, the species vary in their farming-arts, and *C. strigatus* is more advanced than *auritus* in her mode of producing kohlrabi.

It can be easily understood, says Möller, that when the mycelium remains short but becomes swollen it is more agreeable, convenient and nutritious for the ants and their brood than a mould with long filaments. Thus the cultivation of fungus - mycelium, the regular cutting-off of the mould-filaments and their partial transformation into kohlrabi in the phylogeny of the *Attini* can be explained by natural selection and the inheritance of acquired characters. In this hypothetical

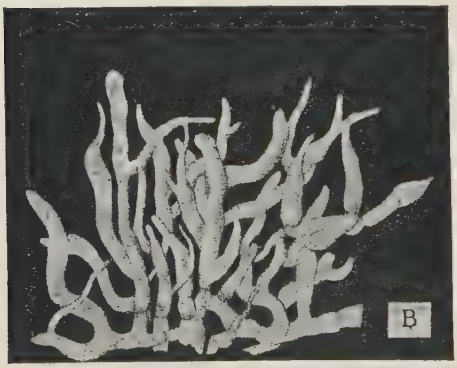

Fig. 117 B

phylogeny *Cyphomyrmex* occupies the lowest rung of the ladder, *Apterostigma* the middle rung and *Acromyrmex*, especially *Atta*, the top. Fig. 117*B* represents a garden or rather medley of kohlrabi belonging to *Cyphomyrmex strigatus*. In those of *C. auritus* the swellings are still less marked, and the kohlrabi less abundant. These two species eat each other's kohlrabi and refuse those of *Apterostigma* and *Acromyrmex*. The brood of *Cyphomyrmex* is housed in the meshes of the fungus garden, and so are those of *Apterostigma*, *Acromyrmex* and *Atta*.

Möller gives us no suggestion as to the kind of fungus to which the mycelium of *Cyphomyrmex* must belong.

Möller's researches reveal one fact of capital importance, namely, that the higher *Attini*, at any rate—*Acromyrmex* and *Atta*—are incapable of subsisting without their fungus-gardens, and that *Rhozites gongylophora*, moreover, appears to be similarly circumstanced, that is to say, appears to be unable to live or reproduce itself without the *Attini*. Here, therefore, we have a case of true complete symbiosis, in which neither of two living beings adapted to each other can live without its complement. For further details on this subject I will refer the reader to Chapter I of Part I and also to Chapter III of Part II. We now pass on to later investigations.

During my Colombian trip of 1896 I was unable to stop anywhere for a sufficient length of time to study the habits of the *Attini*. Apart from the large *Atta* already mentioned above, however, I have made various short observations on various species and genera, which are as follow:

Acromyrmex octospinosus, found in the heart of the virgin forest while we were camping out in the clearing of 'Narancho,' and at Dibulla. It builds its fungus-gardens without any openings, between the grasses and the

brushwood spines, but in the open air, as observed also by Goeldi. At Dibulla I found a nest in a hollow tree.

Acromyrmex aspersus var. *Santschii*, of the forest near Sta. Marta. Its subterranean nest opens by a crater and possesses an unique fungus-garden, situated fairly deep down in the earth.

The sub-genus *Trachymyrmex* is related to the typical *Acromyrmex*, but is fundamentally distinguished from it by the absence of polymorphism in the worker. Consequently all the ☿ do the same kind of work in connection with the cultivation of their fungus, whose species is unknown. Possibly they still use—or, as we ought to say, have reached the stage of using—*Rhozites gongylophora*. In 1899 I found a fungus-garden of *Tr. septentrionalis*, as large as an egg, lying buried, but almost on a level with the ground, in North Carolina. The ☿ carried fragments of this and even used them as defensive screens against me, and against the *Cremastogaster* which I placed in front of them.

Tr. Marthæ, found at Sta. Marta on February 19th, in the shade of a mangrove, *bringing flower-petals to its nest*. This structure was mined in the earth, and opened *above* the ground-level by an abrupt tube of masonry, similar to that of *Tr. turrifex*, represented in fig. 46 (Part II) and to that of *Möllerius Landolti*. I was obliged to dig 4 centimetres down to find the fungus-garden and the winged sexes. The fact that *Tr. Marthæ* was carrying flower-petals seems to indicate that it begins, at any rate, by cutting them.

Tr. Cornetzi, *Irmgardæ* and *Bugnioni*, discovered by myself in the same regions of Colombia as *Tr. Marthæ*, nest in the same way and form a slight transition to *Myrmicocrypta*, which also belongs to the *Attini*.

Mycocepurus Smithii. I came upon a polycalic formicary of this species at Dibulla in Colombia, in some sandy

soil at the foot of a bush. The nests had several craters, and their fungus-gardens were somewhat ill-formed and shallow but very neat. *Mycocepurus* drags home dry leaves and

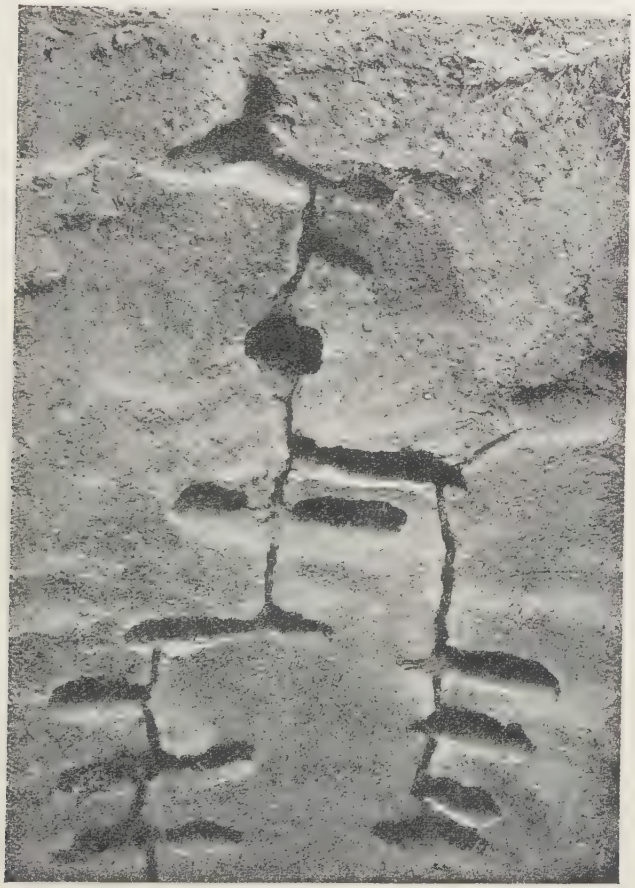

Fig. 121

caterpillar excrement. According to Möller, its mycelium is different from *Rhozites gongylophora*.

I found *Cyphomyrmex atratus* in a decayed trunk, but I

could not discover fungus-gardens belonging to either this species or *C. minutus*.

Sericomyrmex Diego. I found this species on March 3rd, 1896, in the humus of the forest at Don Diego, at the foot of the Sierra Nevada of Santa Marta. The nest had a crater composed of large earth-grains. Under the ground these ants had built a beautiful fungus-garden two centimetres deep. The *S. Diego* gathered small green masses of vegetable substance, resembling an alga, and combined it with other débris to make her fungus-garden, in which I found ☿ and winged ♂.

While I was in Burghölzli-Zürich in 1894, Mr. Urich of Trinidad sent me some live *Acromyrmex octospinosus*, with their fungus-garden. I managed to keep them alive for a month, and used them in partial confirmation of the perfect accuracy of Möller's observations. They hastened to dig themselves a charming round chamber in the earth, quite near the surface, and to transport their fungus-garden thither.

Like *Acromyrmex*, but to a less extent than *Atta*, the subgenus *Möllerius* has polymorphic ☿ which cut leaves, from whose booty it makes its fungus-gardens. For fig. 121, which represents the vertical section of the subterranean nest mined by *Möllerius Silvestrii*, we are indebted to Dr. Bruch. In the lower left-hand corner, in one of the lateral chambers of the left vertical passage, branching down from above, a fungus-garden is distinctly visible. On comparing this figure with fig. 112, which represents the granaries of *Oxyopomyrmex*, after Santschi, every reader will be impressed by the analogy between the arrangement of these granaries and that of the fungus-gardens.

Wheeler agrees with me in regarding *Cyphomyrmex* as the most primitive of the *Attini*. At one time he even declared

that the fungus-gardens of *C. rimosus* were only temporary. He tells us that this species builds its nest under wood or stones and manures its fungus-gardens with caterpillar excrement. They are built in compact, yellowish, irregularly polygonal or pyriform bodies, measuring 25–55 millimetres in diameter, and these masses consist of elliptical cells similar to those of the yeast plant (*Saccharomyces*). Wheeler has drawn this fungus, which he has named *Thiridiomyces formicarum*.

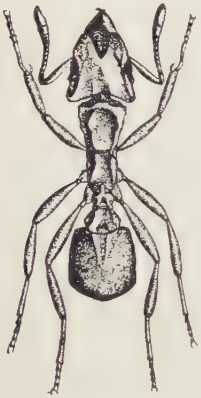

Fig. 122

C. Wheeleri, of fig. 122, is a nocturnal Texas species which picks up small fragments of plant-débris and grows upon them a snow-white, flocculent mycelium, as well as masses of kohl-rabi. These small fungus-gardens lie on the floors of small dilations in the earthen galleries which make up the nest. Those of both *Cyphomyrmex* and *Mycocepurus* are irregular, and never suspended.

Mycetosoritis makes small vertical passages in the sand, as much as 75 cm. in depth. These passages suddenly dilate to form 2–4 round chambers, 1·3–3·4 cm. in diameter, in which the garden is hung from a rootlet, arranged by the ants for this purpose.

According to Wheeler the fungus-garden of *Trachymyrmex* is pendant, like that of *Mycetosoritis* and *Apterostigma*, which it resembles, save that in the case of *Tr. septentrionalis* it is more regular and spread among various chambers of the branching passages. The mined nest of these various ants is surmounted by either a tube or a crater.

Von Ihering thinks that the cultivation of fungi by the *Attini* must be derived from the harvesters by a transference

of appetite from the hard seeds to the delicate fungi, and Wheeler considers that the analogy we have just pointed out between the fungus-gardens and the granaries of *Oxyopomyrmex* renders such a hypothesis very tempting; for my part, however, I remain very sceptical in this respect. The nearest relations of *Cyphomyrmex* and *Mycocepurus* are not the harvesters, but other genera, *Basiceros*, *Proatta*, etc.

Colony-Foundation among the Attini. This brings us to the origin of the *Attini* colonies. In Part III, Chapter II, where a similar subject was discussed in connection with other ants, we decided to reserve the answer. So here we are faced by the perplexing question: Does the first *Rhozites* garden owe its origin to the colony-queen, and if so, in what way?

In 1894 Sampaio discovered the queen with a fungus-garden in an incipient formicary of *Atta sexdens*. But Ihering was the first to prove this all-important fact: when any virgin *Atta sexdens* ♀ leaves her nest for her nuptial flight, she takes with her in her buccal pocket (Fig. 5*D*, Part I) a small pellet from the fungus-garden, half a millimetre long, the unexpelled refuse of her last meal. This, then, is a dowry which she takes from the maternal formicary without asking permission. Directly she is fertilized she does as nearly all ♀ ants do—rids herself of her wings, digs herself a chamber in the soil or humus and shuts herself in it. But there her first care is to spit out her pellet of hyphæ into a corner of the chamber. Our *Camponotus*, *Lasius*, *Myrmica*, *Messor*, etc., do nothing of this kind. Like them, she lays eggs; but side by side with the eggs a pretty little fungus-garden can be seen gradually springing up—a very dainty thing, which Madame *Atta* tends like the apple of her solid composite eyes, and much better. She tends it like a lady who is growing a geranium in her window-bay; in other words,

she pampers it as an old maid tends, combs and fondles her cat, and on no account will she eat a morsel of it.

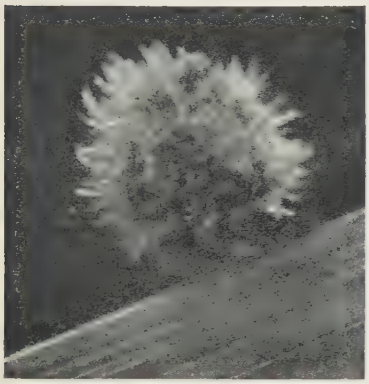

Fig. 123

This fungus-garden flourishes, passing through the three stages which we see in figs. 123, 124 and 125 (*Acromyrmex Lundi*), after the admirable original photographs twenty-five times enlarged, which their maker, Dr. Carlos Bruch of La Plata, was good enough to send and allow me to utilize here. Fig. 123 represents the beginning of the garden, soon after the pellet is thrust out. In figs. 124 and 125 we see some eggs laid by the ♀ and placed close against the garden.

But what does the queen use as food for this crop? Ihering and Goeldi thought that she took some of the eggs she had laid, crushed them and made them into manure. Many of the eggs which are laid do presently disappear; Nevertheless, these authors were wrong.

We are indebted to the classic researches of Dr. Jakob Huber, a young Swiss, Dr. Goeldi's assistant in the Goeldi Museum at Para, for elucidating the matter and watching the initial formicary founded by an *Atta sexdens* ♀, until the very last stage in its development.

J. Huber and Goeldi were the first to observe the way in which *Atta* feeds its larvæ from the fungus-garden. In 1905 Goeldi constructed a glass-covered artificial nest which enabled every movement of the colony-queen in her chamber to be observed. It was with this and similar apparatus that J. Huber made his meticulous observations, continued from

day to day. As a rule, the fertile *Atta* ♀ fight and mutilate each other when put together. Once, however, Huber managed to induce an alliance between two of them, which even joined forces to build their fungus-garden until the ☿ were hatched.

Fig. 124

The day after the nuptial flight the ☿ spits out the contents of her buccal sac, which constitute her dowry, into her natural or artificial chamber. Here we may note that the buccal pocket of the ♂ which flew away with her is always empty; these ♂ take no dowry with them, as Huber has

proved. That which the ♀ expels is yellowish or even black, ·5 mm. in diameter, and scarcely visible against the floor of the chamber, but by pulling the mouth of the ♀, Huber succeeded in inducing her to emit under artificial conditions. On the third day he saw that five or six eggs had already been laid, and the pellet at their side had become white with

Fig. 125

mycelium filaments, forming a little ball 1–2 millimetres in diameter, like that in fig. 123—which, we must not forget, is magnified twenty-five times. During the days that follow Madame *Atta* divides this little ball into several fragments, as seen in figs. 124 and 125, and the number of eggs laid increases irregularly to ten a day, for ten or twelve days.

The eggs, which at first were kept separate, are now placed on or among the flocculi. *A. sexdens* has more than a hundred, but *Acromyrmex Lundi* of fig. 124 and 125 has much less.

In 14–16 days' time the larvæ begin to appear and the fungus-garden becomes 1·2–1·5 cm. wide. The first nymphs are seen about a month after the ♀ enters the chamber, and they are 1·5–3·5 mm. long. The fungus-garden then attains a length of 2 cm. and at last begins to produce kohlrabi clusters. A week afterwards there are about thirty nymphs, the first of which are ready to hatch. These are pygmy ☿, which at once begin to tend the larvæ and nymphs, like the ♀, and eat the kohlrabi, as their mother has never done. Sometimes the entire development is slower, and may require more than two months.

But how do the fungus-garden and brood of the *Atta* queen contrive to increase to this extent? After observing the ♀ for several hours, Huber saw her tear off a small fragment of the fungus and hold it against the tip of her gaster, which is bent forward for this purpose; at the same time she emits from her vent a clear brownish drop which

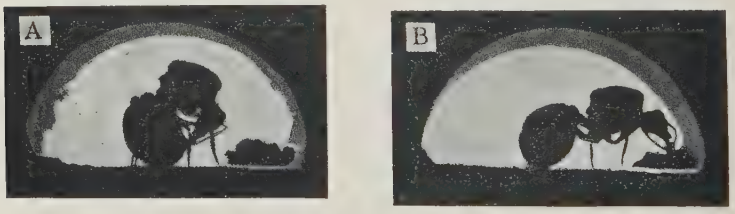

Fig. 126

is immediately absorbed by the tuft of hyphæ. Fig. 126*A*, taken from an original photograph by Huber, shows this performance on a life-sized scale. Having thus manured the fragment with her own excrement, the *Atta* ♀ thereupon

a. *Polyrhachis* (*Myrma*) *Horni* ☿. Ceylon.

b. *Polyrhachis Ypsilon* ☿. Sumatra.

c. *Polyrhachis* (*Chariomyrma*) *appendiculata* r. *Schoopæ* ☿. Australia.

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c. Polystemum (Cistineæ) obbemiense n. sp. Arabia.

p. Polystemum Jonis n. sp. Arabia.

s. Polystemum (Malveæ) Horsfordii n. sp. Ceylon.

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places it in some part of the fungus-garden, as shown in fig. 126*B*, compressing it between her front legs as she does so. The fungus absorbs the manure more or less rapidly, and the yellowish remains of these droplets can often be seen in several places on a fungus-garden. Huber says that a performance like this is usually repeated once or twice an hour. When a piece of fungus is given to a fertile *Atta* ♀ which has not hitherto possessed one of her own, she probes this unexpected gift with her antennæ, in evident excitement, divides it into several fragments, and begins in a few moments' time to manure it with her excrement in the manner described and illustrated above.

It is certain, therefore, that the growth of the fungus-garden is due to the manure supplied by the *Atta* ♀, consisting of her excrement, probably enriched by the secretion of some gland, rectal or otherwise, and according to Huber, this manure lasts as long as the cenobitic phase of the colony-queen's life.

But that is not all; Huber attentively watched the egg-laying process, and ascertained definitely that no sooner has Madame *Atta* laid an egg, which she does constantly, than she probes it, puts it in her mouth and swallows it without further ceremony. She even licks her legs blissfully when this operation is finished. Huber calculated that during the first period of incubation the ♀ swallows at least two eggs an hour, and lays about fifty a day. Assuming that forty days elapse before the first ☿ hatch, he estimates that about 2,000 eggs are laid, and that accordingly 1,800 are swallowed, as against a bare 200 which are reared as larvæ, nymphs and ☿. This, dear reader, is indirect adelphophagy (see Part III, Chapter II) in the form of ovophagy (swallowing of one's own eggs), and at this stage it begins to be of serious account. When all is said, therefore, the *Atta* ♀

feeds her progeny and fungus with substances produced by her own body, especially by her large, fat abdomen and the strong re-absorbed muscles of her fallen wings. These substances are transformed into manure for the fungus and into eggs which are laid and then eaten or raised into larvæ.

But over and above this Huber managed to see how Madame *Atta* feeds her larvæ *directly* with the eggs she lays (direct adelphophagy). She strokes a larva with her antennæ until it opens its mandibles; she then seizes a new-laid egg and thrusts it against the larva's mandibles, and on to its gaster, whereupon it is eaten. If the larva is young and small, the ♀ then gives the rest of the egg to a second larva, but if it is large it consumes the whole egg in three to five minutes. Huber saw four eggs administered to various larvæ in two hours, and on one occasion even eight in the same space of time. He never saw the ♀ eat kohlrabi clusters from their gardens or give them to their larvæ. Madame *Atta* is a good gardener, but she never eats kohlrabi, even from other nests, while she is the mistress of her own house. She can also rear her brood without fungus, as Möller once managed to observe while watching an artificial nest till the workers were hatched.

With the appearance of the first small ☿ (2–3 mm. long), the scene begins to change; the ☿ take charge of the nymphs, and for a certain length of time they also continue to feed the larvæ and their common mother herself with the eggs she lays. Like this queen on a small scale, they manure the fungus-garden with little drops of their excrement—a very amusing performance to watch, so Huber tells us. But on the other hand they begin to eat the kohlrabi on their own account, and sometimes several set to work to suck the drop from one of their number, after manipulating it between their mandibles.

About nine or ten days after the first ☿ are hatched larger ☿, 4–5 millimetres long and with larger heads, come out in their turn from their nymph-skins. Not until this moment do the ☿ of all sizes begin to mine the earth in several directions at the same time, building passages about 2 millimetres in diameter to bring them to the surface and form a crater which opens outwards. At this moment Huber presented them with some rose-leaves which the largest instantly began to cut up in a most methodical fashion, by an innate instinct. Such were the first stages in the definitive construction of the fungus-garden, seven weeks after the queen began her cenobite life.

Goeldi was the first to observe the manner in which the pygmy ☿ sow the mycelium and its spores on the smallest fragments of leaves, which have been cut and re-cut by their big sisters. The workers then cease to manure the fungus with their excrement. The mother, for her part, finds some difficulty in accustoming herself to the new method, and seems as though she were sulking in a corner. She is no longer allowed to eat her eggs, which are taken from her as soon as she lays them; and her cherished fungus-garden, reared as lovingly as any window-geranium, now grows without receiving manure from her! For the sake of peace she resigns herself to the inevitable, and is finally compelled by hunger to allow herself to be fed by the ☿ with the kohl-rabi and fungus which she has always delighted in licking but has never desired to eat. Goeldi and Huber saw this happening in the older formicaries. In short, she gradually sinks to the level of a 'reine fainéante' or laying-machine.

It is hardly necessary to say that the fungus-garden then grows larger and the ☿ pierce large holes in it wherein to house the whole brood. In short, the nest gradually

develops like that of *Atta columbica*, which I have already described.

I must own, however, that one point is not yet clear to me, and that is, how the fertile ♀, the solitary guardian of the fungus-garden, prevents the mycelium from invading every point of the cell, like the one I saw spreading about my cigar-box in Colombia after the removal of the workers, and stifling her, as it stifled some ☿ described by Möller. Huber never states that she herself cuts the mycelium filaments. Those shown in our figs. 123, 124 and 125, after Dr. Bruch, do not look as though they had been cut. This matter must be elucidated at some later date.

Again, no one, so far as I know, has yet attempted to starve *Attini* and feed them with honey or dead insects. Assuming that *Atta* and *Acromyrmex* will die of hunger rather than touch any such food, we do not know that this is also the case with the primitive *Attini*, such as *Cyphomyrmex*. There we have a few experiments still to be tried.

Anyhow, you must admit, dear reader, that the life-history of the *Attini*, as revealed by such conscientious and distinguished naturalists as Belt, Möller, J. Huber and Bruch, is among the greatest wonders known to us, in respect of adaptation by the natural phylogeny of instincts, produced by the symbiosis of certain ants with the fungi they cultivate. The culminating point of this wonder is the way in which the fertile female rears, cultivates and manures, but omits to eat, the substance she brings with her as her dowry, which is destined eventually to support her posterity as well as that of the fungus. There are the patent facts, and we must beware of altering them to suit our hypotheses!

While in Sumatra, v. Buttel-Reepen discovered the new genus *Proatta*, which is closely related to the true *Attini*, and lives in termite nests. But it does not grow fungi.

Bruch's Researches on the Attini

Dr. Carlos Bruch has continued his admirable researches, which I may here summarize. He has just published some of them in Spanish (*Estudios Myrmecologicos*, *Rivista dal Museo de la Plata*, Vol XXVI, p. 175–211, Buenos Aires, 1921).

In the first place, with the aid of Dr. Spegazzini, he distinguished the three species of fungi peculiar to the Argentine *Attini* and entirely different from Möller's *Rhozites gongylophora*.

1. *Locellina Mazzuchi* Speg., peculiar to the large *Atta Vollenweideri*. The cap of this enormous fungus may attain a diameter of 42 centimetres, and the whole may weigh as much as 3 kilogrammes. It seems to grow only on *Atta* nests.

2. *Poroniopsis Bruchi* Speg., which grows on every nest of *Acromyrmex* (*Möllerius*) *Heyeri*. Here Bruch is very emphatic, and declares that the fungus lives *exclusively* on and in the nests of *Möllerius Heyeri*, which are never without it, and outside of which it is never found.

3. *Xylaria micrura* Speg., which grows on the nests of *Acromyrmex Lundi*.

Thus it is plain that the more closely we study the matter, the more cases of symbiosis we find between various species of *Attini* and various genera of fungi. Bruch, however, also made other experiments. I had advised him by letter to try giving various *Attini* some honey to eat, and he obtained the following unexpected results. He had previously fed a formicary of *Apterostigma Bruchi* so well that numbers of ☿ would come to him when he approached, take directly from him the caterpillar excrement he offered them on the end of a platinum pin, and carry it to their fungus-garden. But it was in vain that he offered them the débris of various plants, except a concoction of maté, which they promptly

utilized for their fungus, whereas they rejected all other leaves.

After he had starved a colony of *Acromyrmex Lundi* for three days Bruch gave them a little honey on a sheet of glass. They soon began to lick it up, and continued thus for five to six minutes, without befouling themselves unnecessarily. They were then placed near another ☿ which had also fasted, and she hastened to lick their mouths. These experiments were continued for nearly a fortnight. The ants which were fasting languished, and eventually died, but those which had been fed entirely on honey remained active and well. Hence it is clear that *Acromyrmex* can remain alive when fed on honey—a fact hitherto unknown.

Bruch renewed his experiments with honey, and the result was identical. He then gave his starving *Acromyrmex* some sugar moistened with water. The result was remarkable; all the ☿ gathered round the sugar and spent half an hour eating it; it was evident that they greatly preferred it to honey. Mutual regurgitation followed.

An experiment with the white of an egg—a substance which the *Acromyrmex* seemed not to perceive at a distance with their antennæ—was only partially successful. The ☿ stuck in the middle of it. Afterwards, however, Bruch saw them licking the white of egg. On the other hand, they turned away in disgust and even made angry threats when Bruch offered them a *ragoût* of mashed earth-worms. In contrast to this, they licked the juices of a beetle.

He then repeated his experiments with the large species *Atta Vollenweideri* (see fig. 127). Figs. 115 and 127 show sections through the nest and fungus-gardens of the Argentine *Atta Vollenweideri*, photographed by Bruch (who appears in person in fig. 127 to show comparative heights), using sugar and honey. The *Atta* were more

sociable but clumsier than the *Acromyrmex*. They flocked round this unaccustomed food, licked it up and disgorged it to each other. A very similar result was obtained in the case of *Apterostigma Bruchi* with maté, sugar and honey.

Summing up, therefore, we may say that the *Attini* can be artificially fed, after fasting, with sugar, honey, a confection of maté, and even finely-ground insects or white of egg.

Fig. 127

This is evidently the result of an ancestral phylogeny of instinct, analogous with that of *Strongylognathus testaceus*, cited in Chapter I of Part I, and towards the end of Part IV. Obviously the ancestors of the *Attini* must have fed on sweet substances and insects before they began to develop their instinct for fungus-growing

We have still to learn whether the *Attini* and their

colony-queens could manage to feed their brood with sugar, honey, etc.

Dr. Bruch furthermore makes the following interesting observation on *Acromyrmex Lundi*. On December 11th the nuptial flight took place. A week later, as he was passing near the same nest, he saw a crowd of ♀ running about with their abdomens cut off. Several of them were still being followed by their ☿, which were coming out of the nest-entrance; the abdomens of the ♀ were cut off behind the post-petiole. But why?

At the beginning of November he also saw some winged ♀ (virgins) of *A. Lundi* walking among their ☿ and gathering some fallen seeds with them.

Finally, he imprisoned two fertile *A. Lundi* ♀ in the same chamber. By mutual agreement they made a garden together from *a single pellet* (which they had presumably ejected) in order to cultivate their fungi, and here they both laid their eggs.

Chapter IV

WEAVING ANTS

It has long been known that certain ants, such as *Œcophylla*, *Polyrhachis* (see Plate XV, *a*, *b* and *c*) and a few *Camponotus*, all members of the sub-family *Formicinæ*, dwell

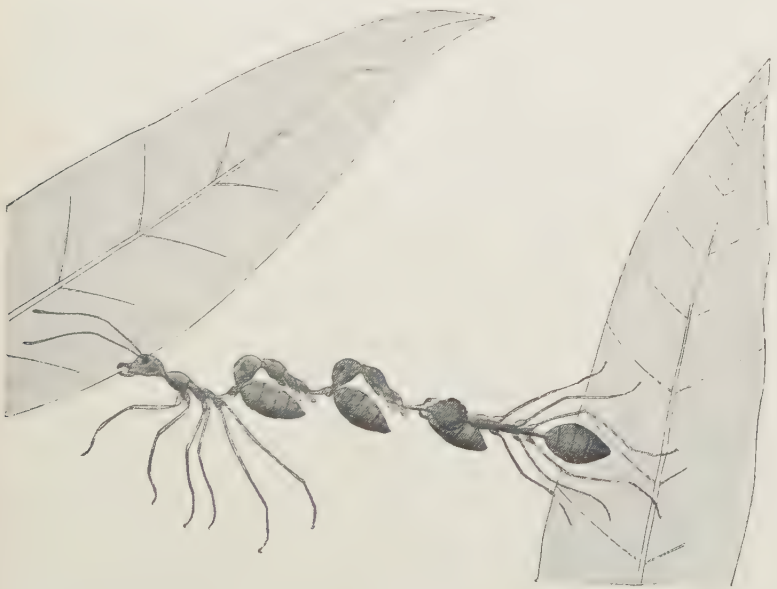

Fig. 128

in nests of finely woven silk. At one time, misled by Aitken's faulty observations in India, I thought that the *Œcophylla* wove their silk for themselves with a secretion of

their own maxillary glands, hardened in air, as our spiders do, and as other ants apparently weave their carton.

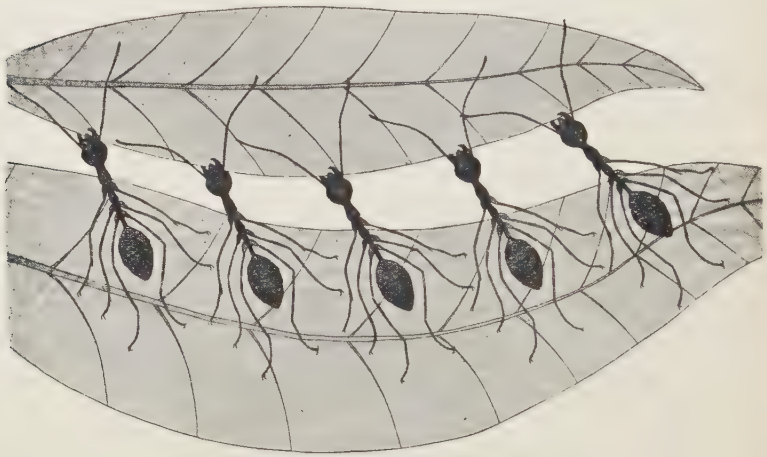

Fig. 129

Fig. 130

This, however, was an error.

The truth—and a most interesting truth — was discovered in 1890 by Ridley, and afterwards confirmed by many other observers. Fig. 131, borrowed from Doflein, and Bugnion's more recent figures (128, 129, 130), will be more efficacious than anything else in helping my readers to understand that the *Œcophylla* weave their silk by utilizing their own larvæ as a weaver uses his shuttle. Every worker seizes a larva in her

mandibles, and, together with her squad of companions, which are doing likewise, carries it to a place between two

Fig. 131

leaves, fixing its mouth to the edge of one leaf, as shown in the lower part of fig. 131. Meanwhile another squad of *Œcophylla* ☿ pulls with all its strength to draw one leaf

Fig. 132

towards the other, each ☿ grasping it by the one edge and hanging on to the other with all six legs at the same time.

The final result of the workers' admirably co-ordinated efforts may be seen in fig. 132, firmly connecting three leaves. The extremely close and regular silken tissue *G* spun by the larvæ and woven by the *Œcophylla* ☿ is depicted in our illustration. The best idea of the matter will be got from fig. 133, after Doflein, which represents in *B* an *Œcophylla smaragdina* larva with its enormous silk glands. By way of comparison, fig. 133*A* shows a *Tetramorium cæspitum* larva, which does not spin a cocoon; but *Lasius flavus*, which does so, has silk-glands scarcely any better developed than those of *T. cæspitum*. This proves that the weaving of the nests exacts much more silk from the larva than the manufacture of a cocoon, an operation which only takes one day in an ant's life. The silk-glands are shown in fig. 133 in dark stipple. When the leaves are so far away from each other that their edges cannot be seized by the same *Œcophylla* ☿, these ants form chains, each ant taking hold of another by the back of the petiole, until the first is able to hold one end of one leaf-edge in her mandibles, and the last to hold the other end of the other edge between her six legs. Both then pull the two leaves towards each other, while the other squad of ants weaves with its larvæ, if necessary, utilizing the chains of the first squad as a bridge. Dodd has observed this last fact in Australia in connection with

Fig. 133

Œ. virescens. Prof. Bugnion's sketches are from his pamphlet *l'Œcophylla de Ceylan* (*Bull. Soc. Zool. France*, 1925).

The extremely common nests of *Œcophylla* in Asia, Northern Australia and Africa are not artistic; these ants simply fasten a number of leaves together without weaving chambers. Among the leaves thus enclosed by the silken threads they casually spread their brood and winged sexual forms. We have here a fact almost unique in nature, except in man—the use of one living creature by another as a working tool.

In the journal *Tropenpflanzen*, 23rd year, No. 5/6, 1920, p.142, Karl Friederichs relates how the natives of Eastern Asia, particularly Cochin-China, scrupulously respect and tend *Œcophylla smaragdina*, since it protects plants and fruit from the attacks of noxious insects, and have no faith in the other remedies of our European tree-growers. Friederichs' own researches have led him to confirm, to a large extent at any rate, the opinion of the natives. He even thinks that the *Œcophylla* do useful work in removing coccids from oranges and cultivating them under their own care. I have serious doubts on this score, but for the rest I refer the reader to Friederichs' interesting work.

Fig. 134 represents the fabric woven by *Polyrhachis* (*Chariomyrma*) *Jerdoni* in Ceylon, with the aid of its larvæ, between the débris of leaves. The most industrious *Camponotus* weavers undoubtedly belong to the sub-genus *Myrmobrachys* and the species *senex*. Goeldi sent me a nest belonging to this last species, which is a veritable gem. It is triangular in shape, 21 cm. high, 10 thick and 18 broad at its base, and is perched on the twig of a tree, between whose leaves it is woven. But far from being shapeless it is composed of a myriad little superimposed chambers, each about one centimetre broad by half a centimetre high.

These chambers are connected by small columns and by walls, as in the nests built in the earth or woven out of carton, The extraordinary fact about it all is that the chambers, columns and walls are all finely woven of pure silk by the aid of larvæ! The tissues are close and firm though exceedingly light. Goeldi himself observed *C. senex* re-weaving, that is, mending, by means of the larvæ they held between their mandibles, some of their chambers which he had slightly torn. I have the nest in my collection. Best of all, this nest contains in its interior another nest, built by *Melipona*, a small genus of American bees, and enclosed by *C. senex* between the fabric of their own nest and the leaves on the twig. In this case, *C. senex* and *Melipona* were living in peaceful parabiosis.

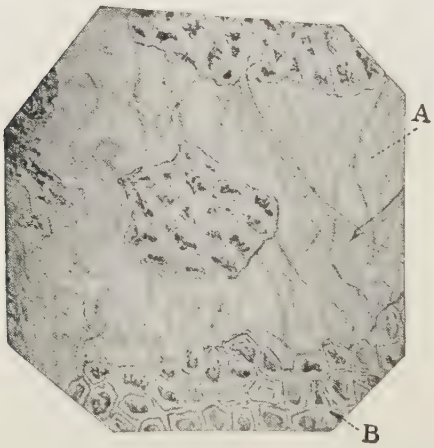

Fig. 134

For varied work of this kind, the large genus *Polyrhachis* and its numerous sub-genera must be awarded the highest honours. Nearly all these ants construct all manner of nests, often forming infinite *combinations* but no *mixtures*, with carton woven by the ☿ themselves; this I have been able to prove by an attentive examination made partly with the aid of a microscope. While weaving with their larvæ, indeed, ants cannot mingle with their fabric, in a single action, the particles of wood-rot, etc., which they stick together with the secretion of the mandibular glands. These two

operations are distinct, but, as we shall see, they can be artificially combined with the rest.

In 1904 Jacobson noted how *Polyrhachis* (*Myrmhopla*) *dives* weaves its nest by means of the slender larvæ which it holds between its mandibles, and repairs any breaches made in the tissue. Taking up the ant on a brush he drew her farther away from the nest, and obtained a good view of the larva functioning as a spinning-wheel. The nest of this ant, like that of *Myrmobrachys senex*, is composed of a number of chambers, but its brownish fabric is intermingled with the débris of leaves, dry stems, bark, etc., which she binds together as she weaves. It resembles a carton nest, though it is quite a different thing. Like that of *P.* (*Chariomyrma*) *Jerdoni*, depicted in fig. 134, it is perfectly supple, like cloth. Inside this nest *P. dives*, which is not carnivorous like *Oecophylla*, keeps coccids as milch-cattle. Jacobson found specimens between the leaves of a palm-tree, and also on the ground between grass-stems. Underneath some leaves he also saw small succursals, serving as coccid-sheds, all woven like the principal nest. I will refer the reader, moreover, to Part II, Chapter VI, sec. 6, particularly in connection with mimicry in the nests of *Polyrhachis* (*Myrmhopla*) *pressa*.

Here I merely wish to enumerate the variations and combinations in weaving which we find in the nests of different species belonging to the large genus *Polyrhachis*, not to mention the sub-genera. From Java and Ceylon, in particular, I have received a number of interesting *Polyrhachis* nests, sent me by Jacobson and Bugnion, most of them being *unilocular* (formed of a single chamber) and a few *multilocular* (formed of several chambers). According to Jacobson, the *Polyrhachis* carry each other in the manner of the *Camponotus*.

1 NESTS ENTIRELY WOVEN:

Polyrhachis bicolor of Java weaves a unilocular nest, with very loose meshes, like a spider's web, under a leaf or between several leaves; a few fragments of dried leaves can just occasionally be seen caught up between the threads. According to Karawaiew, *P. Mülleri* makes a very similar nest, though with a close woven fabric.

P. simplex (*spinigera*) of India and Asia Minor weaves a unilocular nest of close, fine, light-red fabric, which, as Wroughton has proved, forms the lining of a cavity lying entirely underground.

2 WOVEN NESTS COMBINED WITH VARIOUS MATERIALS:

We have just described the multilocular nests of *P. dives*, and in Part II, Chapter VI, sec. 6, we described the mimetic nests of *P. pressa*, with their pillars. *P. arachne* of Java, *Jerdoni* of Ceylon, *Dahlii* of New Britain, etc. make unilocular nests of a very loose tissue, intermingled with plant-débris which are often fairly large like those in fig. 134, and situated on or under the leaf of an ordinary tree—a palm, bamboo, etc.

P. rastellata, *tibialis* v. *parsis*, etc., of India and Java, make nests very similar to the above, but the fabric and more especially the materials are more compact, so that the daylight can hardly be seen between the débris bound up in the woof.

3 NESTS COMBINED OF SILK AND CARTON:

The unilocular nest of *P. thrinax*, *furcata* and *Frauenfeldi* in India and Java has such a strong fabric, woven in its leaf, and the carton covering the *open* interstices is so fine, that we may well ask whether it does not consist merely of pieces of very fine material, joined together by the fabric which covers them on the underside, and whether it is carton at all.

On the other hand, in the case of *P. Jacobsoni* and *Schang* v. *parvicella* of Java, of *hippomanes* r. *ceylonensis* of Ceylon, *Mayri* of India, etc., the matter is much more obvious; a single chamber, usually large—sometimes very small—opens by one or several little holes. But if the nest be separated with great care from the leaf, a woven weft, which is all that covers the leaf, comes away with it. With the aid of a microscope this weft may be seen to continue under the carton. The ants must therefore *begin* by weaving the weft with their larvæ, and afterwards cover it with carton; I can scarcely believe that the inverse process is possible.

P. Solmsi v. *multicella* of Java makes on or under a leaf some fair-sized multilocular nests composed of three or four large chambers, each communicating with the outside by a separate hole. The inner side of each is lined with woven silk, covered by rather fine and flexible carton—somewhat doubtful, like that of *P. Frauenfeldi*, *thrinax*, etc.

4 POLYRHACHIS NESTS WHICH ARE NOT WOVEN OR DOUBTFUL:

In Part II, Chapter VI, I have described the *twisted* tubes made by *P. Zopyrus* (Java) out of rolled grasses. *P. Orpheus* (Java) makes similar nests out of various débris stuck together, in which the weaving seems to me problematic. *P. Lilianæ* of Java and *scissa* of Ceylon do likewise.

The nests of the African *Polyrhachis* are little known. I possess one made by *P. Gerstäckeri* in a gall-nut. It is probably lined with silk or carton, but its remains are not sufficient to make this certain. According to Dahl, the nests of *P. Cyrus*, *arcuata* and *relucens*, New Britain, are simply mined in the earth or between the roots of parasitic plants, and contain no silk or carton.

There is one more genus of ants, *Technomyrmex*—this time belonging to the *Dolichoderinæ*—which possesses a

species living in small woven nests, imitating lichens. This is *T. bicolor* r. *textor*, found by Jacobson in Java in 1909, and its nest seems like a reproduction in miniature of the *Polyrhachis pressa* nests described in Part II. It is 2 cm. long, 1 cm. broad and a few mm. high, and forms a single little pocket of woven tissue intermingled with plant-débris, covered with a greyish lichen and attached to the bark of a tree.

How ants first began their weaving process is an interesting speculation. They are careful to clean off the earth which adheres to the cocoons spun by the larvæ. Now it is a well-authenticated fact that the thread which comes out of the mouth of *Polyrhachis dives*, for example, is viscous and often sticks to other threads, with which it forms bridges or anastomoses. Probably such facts as these may have led certain species to solidify their carton by the aid of the larvæ which were weaving their cocoons. Here we can only offer conjectures. But with regard to the origin or phylogeny of the instinctive art of nest-weaving by means of larvæ, we can here offer nothing but conjectures; so we should be wiser to hold our peace.

Chapter V

ANTS AS JANITORS

I use the term 'janitors' with reference to the ♃ or large ☿ porters whose special duty it is to guard the doors or openings of a nest, whether it be constructed in the earth or in a stem, or excavated in wood. Carton-nests, woven nests and ant-gardens have no janitors. All those with which I am acquainted belong to the *Formicinæ* or *Myrmicinæ*.

Between the porters which are completely adapted to their office and the semi-porters, there are all possible transitions, and they in their turn, those half-adapted, show all sorts of gradations to the state of ordinary ☿; there is no clearly-marked limit anywhere. Yet the extremes seem almost miraculous. My readers should compare figure *e* at the top of Plate XIV, representing the head of the *Colobopsis paradoxus* worker of Brazil, with figs. *f* and *g*, one of which shows the profile and the other the front view of the head of this same ☿. They will hardly be willing to accept my assurance that these two heads belong to members of one and the same species, offspring of the same mother; yet the fact is incontestably proven. The rest of the two bodies are of the same brown colour and similar in every way. Whence, therefore, this extraordinary difference in colour and shape? Fig. 135 *A* and *B*, which, it is true, represents another species, *C. culmicola* of Jamaica, provides the key to the riddle. Bamboos, which everybody knows, are hollow in

the interior like the Jamaican *Cladium* shown in our figure, but they are of a uniform yellow, not speckled. The nest of *C. paradoxus* is situated in a yellow bamboo of Brazil, identical with that shown in fig. 135*A*. It is pierced by a round hole, probably formed in the first place by the mandibles of the queen, whose head, with its yellow frontal part, is truncated and exactly like that of the ♃. Fig. 135*B* represents the head of the ♃ or ♀ closing the opening and imitating the colour of the stem. This, then, is the phylogenetic cause of polymorphism in the complete porters, ♃ or ♀.

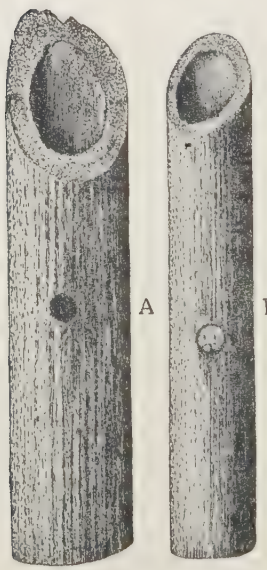

Fig. 135

It was not till after many a fruitless search that I discovered at Vaux near Morges, about 1872, the nest of our European *Camponotus* (*Colobopsis*) *truncatus*. On the withered branch of an old pear-tree I saw a number of ☿ of this species running towards some centre—a mystery to me—situated in the middle of the bark, while no other assemblage of the kind could be seen, either near the foot of the tree or about the top. Knowing nothing about the matter at the time, but stimulated to exceptional keenness by the ill-success of my endeavours to find the home of the *Colobopsis*, I began to observe their movements with concentrated attention. All of a sudden, I saw a very small round hole stand out against the bark, and through this a ☿ promptly slipped in. But, immediately after, the black hole disappeared again, and I saw nothing but the brown rough bark of the pear tree. I thought the effect must have been

produced by a flash of light! Shortly afterwards, a second ☿ behaved in the same way, slipping into another little hole situated near the first, and appearing and disappearing in the same way. But this time I fixed the exact spot, and seizing one of those pins which an entomologist always carries about him, I buried its point cautiously in the hole, which immediately re-appeared. I then slowly withdrew the pin and saw the brown, truncated head of a ♃ advancing once more to take its place as doorkeeper, whence my action had driven it away for a moment.

This incident is illustrated in fig. 136, which shows the position adopted by the *C. truncatus* ♃ as keeper of one of the

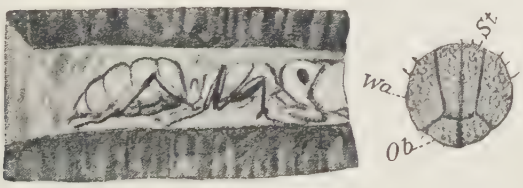

Fig. 136

nest-doors. In the same figure we see a front view of the sculptured part of the head, *Ob* denoting the mandibles, *Wa* the cheeks, *St* the forehead (lower part of the epistoma). The nest in question, sculptured in the hard, dry wood of the pear-tree, contained about 620 ☿, in addition to some ♃ and winged ♀ and ♂. It had no communication with the outer world except by the two small round holes indicated. With my father's permission I sawed off the dry branch containing the nest, which I afterwards presented to the Zürich Museum. But *C. truncatus* is still more commonly found in the dry, hollow twigs of our walnut-trees, or the interior of gall-nuts. *C. etiolatus* of Texas, represented in fig. 65 (Part II), nests in a similar manner, and likewise

admirably hides its entrances to the twigs and galls in an admirable manner by the brown colour and rough sculpture of the ♃'s truncated head. This is a much safer method of protecting the whole formicary than poison or sharp teeth.

According to the species, the head of the ♃ and ☿ of *Colobopsis* and its kindred sub-genera may be shorter or longer and the epistoma entirely or only partially included in the truncated surface of the head. More important is the fact that the truncated anterior portion of the head is by no means always separated from the rest by a sharp *groove*, as in *C. paradoxus*, *truncatus*, etc., nor is it as flat and circular as those in Europe. A whole scale of fine gradations may be observed in the sharpness or bluntness of the edge or the complete or relative flattening of the front part of the head, until we come to the ordinary worker form. Gradations of this kind can be seen even in certain *Colobopsis*, and also in the sub-genera *Myrmamblys* and others.

In this way we pass gradually from the complete door-keeper ♃ to the large ☿ with their great heads, which fulfil the function more or less incompletely and may be described as semi-porters. Forms like this are found in the medium-size ☿ of *Colobopsis Sommeri* of New Caledonia, represented in fig. 137. This species, in fact, possesses all the transitions between a ☿ with an ordinary head and a ♃ with a truncated and blunt-edged head. It is only necessary to observe our *Camponotus herculeanus* and *fallax*, for example, to see how a large ☿ acts as guardian of the nest-doors. She certainly does not close them entirely, and, moreover, she attends to other duties; her colour is neither that of the wood nor that of the earth; the adaptation is therefore very incomplete, but the fact remains. And even the head of the *Camponotus* in question

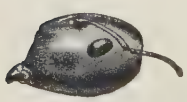

Fig. 137

is much more obtuse in front than that of the sub-genus *Myrmoturba*, for example, whose doors are much less regularly guarded. In *Myrmamblys* and its kindred species, on the other hand, the ♀ semi-porters and large ☿ are clearly differentiated, and keep guard thoroughly. The front part of their head, which is obtusely but more or less distinctly separated from the back part by a curve of varying sharpness, sometimes already has a special adaptation, in the way of sculpture or colour, to the surroundings of the door.

In *Polyrhachis* and the weaving *Camponotus*, however, there is no trace of a janitor or of polymorphism in the worker; so potent is the influence of habits on the form of the body, even when weighed against the real relationship between genera and species. By this means, a comparatively recent phylogeny becomes insidious, concealing a more profound and ancient phylogeny by appearances which are due to adaptation to environment. Thus it happens with the ant-porters and semi-porters.

Melophorus of Australia, one type of which can be seen in *b*, in the middle part of Plate XVI, *Azteca sericea* of the *Dolichoderinæ*, and many *Pseudolasius* species have certain ☿ with enormous heads, very different from the small ☿. But this head is not in the least truncated in front, and very little is known of the habits of these ants. Hence we must defer our judgment. We must, however, suppose, on analogy with the following genera, that these giant ☿ fulfil partially, at any rate, the office of door-porters.

The principal genera of the *Myrmicinæ* possessing ♀ or ☿ with gigantic heads are *Messor*, *Holcomyrmex*, *Pheidologeton*, *Oligomyrmex*, *Atta* and *Pheidole*, and the sub-genera of this last; but in these cases, the head is scarcely ever truncated in front. We saw in Chapter II that the giant ☿ of *Messor* act as an internal police-force, in addition to crushing seeds.

This police-function also involves the guardianship of the doors, which I have observed in various ♃ of *Pheidole* and the giant *Atta* ☿, particularly *A. lævigata* in Venezuela and Colombia, where their large heads may be seen posted in front of every nest-opening.

In connection with the other genera mentioned above, I know of no positive observations on the subject which concern us here, but I think their circumstances are similar. In a few *Pheidole* of the sub-genus *Elasmopheidole*, the head is even truncated to some extent in front.

Species which have no dimorphic workers and no ♃ have ordinary ☿ to guard the doors and close and open them frequently, morning or evening, according to the season. We have already described this in connection with *Formica rufa*, which bars her doors with materials, and other species which use earth. This was the starting-point from which the various polymorphic specializations began in the ☿, including, among others, that of the door-keepers in the genus *Camponotus*.

Chapter VI

THE *RHAGOMYRMICINÆ*

The *Rhagomyrmicinæ* constitute the third section of the sub-family *Myrmicinæ*. We have mentioned them briefly in Chapter V of Part I, and also their three *tribes*, the *Cataulacini*, *Cryptocerini* and *Dacetini*.

The curious forms of these ants can be seen in Plate XIV, *a*, *b* and c, showing the *Zacryptocerus clypeatus* ♂, ☿ and ♀, and also in fig. 138 *A*, *B* and *C*, showing *Cyathocephalus varians* ♂, ♀ and ♃, which represent the second American tribe of *Cryptocerini*. Plate *X*VI *C* shows the no less curious form of the third tribe, the *Dacetini*, which are represented by *Orectognathus sexspinosus* of Australia. As for the first tribe, the *Cataulacini*, the reader has had an opportunity of seeing it in fig. 29 Part I, which shows the two ass-like ears of a fossil ant, *Otomyrmex Silvestrii*.

The first two tribes are very similar, and may be dealt with together apart from the *Dacetini*. Unfortunately we still know very little of their habits. The hard carapace seen in their ☿, ♃ and ♀ is undoubtedly intended to protect them from other ants, as we saw in our first chapter in connection with a war between *Cephalotes atratus* and *Eciton crassicorne*, and also to protect them from other creatures. The countless spines with which their bodies are frequently furnished probably serve the purpose of rendering them indigestible to ant-eaters, birds, etc., which swallow them ; this I suppose

to be the case with *Polyrhachis*, shown in Plate XV, and with others. The question arises as to why their eyes are hidden under the rims of the head, usually in a deep groove called a 'scrobe,' as shown in Plate XV and Fig. 138.

Here, at least, I myself made a positive observation while in Colombia. In Part II, Chapter VI, sec. 4, we saw that the *Cryptocerini* generally make their nests in trees, and often in dead trees. As I watched certain *Cryptocerus* run along the trunk I observed that they scarcely ever went straight in front of them, as other ants do, but—often, at any rate—obliquely or laterally, one leg following the corresponding leg on the other side of the body rather than the forward movements of the two front legs. These *Cryptocerus* sometimes even walk backwards. What may be the origin and aim of their curious motion I am unable to state, as I had no time to follow up my observations. We need scarcely doubt, however, that this oblique or lateral walk is intimately connected with the fact that their eyes, which are often very large, are so placed that they can only see sideways.

Cryptocerus Eduarduli, which I dedicated to my grandson Edward Brooke, in Canada, was discovered in an *Agomanhra brasiliensis* trunk in Paraguay by Prof. Chodat, of Geneva. The nest contained ☿, ♃ and winged ♀. The most curious thing about this species, and, to a less extent, about some kindred forms, is that the eyes of the winged ♀ are much flatter and smaller than those of the worker, which is exactly the opposite of the usual state of affairs in ants. The worker's eye, situated at the back under the frontal grooves, which it overlaps at the sides, is extraordinarily large and convex. That of the ♃ is much less convex, but yet a little more so than that of the ♀. How does this come about? Here I suppose that the ☿ is an active creature which goes out a great deal and probably watches for prey on trees, while the

☙, very different creatures with much more shiny bodies, turn their attention rather to guarding the nest-doors, and the nuptial flight of the ♀, checked to a great extent, takes place in the immediate vicinity of the nest. All this, however, is only conjecture. The *Cr. silvæ* ☿, whose eyes are also very large and very convex, was gathered by myself in Colombia as it ran swiftly over the tree-trunks, but I could discover neither its nest, nor its winged sexes, nor the aim of its marches and counter-marches. There is urgent need of study in the habits of these ants.

In the Colombian forest I saw a veritable army of large *Cephalotes atratus* ☿, with hard armour-plating, attack the nest of some wasps almost the same size as themselves, and steal the brood it contained. The wasps flew round and round, trying vainly to sting, and were overpowered.

With regard to the purpose of the curious form of gizzard in *Cryptocerus* which we discussed in Part I, Chapter IV—a high degree of specialization amid the monotonous uniformity shown by this organ in the rest of the *Myrmicinæ*—we know absolutely nothing.

The ♂ of the *Cryptocerini* are so entirely different from the ☿, ☙ and ♀ that they have been taken for another family of insects. I beg the reader to compare the ♂ of *Zacryptocerus clypeatus* (*a* in Plate I) with its ☿ (*b*) and ♀ (*c*), and also the ♂ of *Cyathocephalus varians* (*A* in fig. 138) with its ♀ (*B*) and ☙ (*C*); we will then see at a glance that they are as different as night from day, the wings and thorax alone indicating their relationship. I possess in my collection an enormous black ♀ of *Cephalotes atratus*, with a broad, square, bordered head, which perished in alcohol, and remains interlocked with her tiny husband. His head is minute and round and his abdomen is reddish. Hence the most sceptical will be forced to believe in the specific identity of ♀ and

♂ *Cryptocerini* which were actually taken together in the same formicary. Strangely enough, a totally different state of affairs obtains with the *Cataulacini;* here the head of the ♂, though small, is not at all unlike those of its ♀ and ☿ in shape and in nature of its spines, etc.

Lastly, a few ♀ and ♃ *Cryptocerini* have heads which are not only broad but hollowed out at the top in the shape of a spoon or an oval plate, and closed, even in front, by the

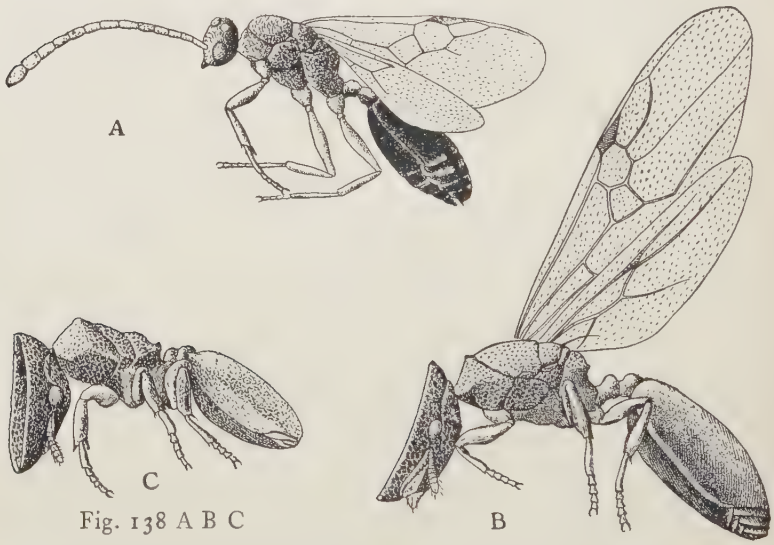

Fig. 138 A B C

two frontal ridges, which entirely cover the epistoma and mandibles when they meet. Fig. 138 *B* and *C* shows this singular phenomenon, which also awaits its interpretation as a result of further study of habits. The head of the *Cyathocephalus varians* ☿ is not spoon-shaped, and resembles that of the ordinary *Cryptocerus*. It is therefore probable that its ♃ and ♀, the sole possessors of the spoon-head, serve for some special office, probably analogous to that of the complete janitors in *Colobopsis*.

The *Dacetini*. In addition to the illustration of *Orectognathus* mentioned above, I refer my readers to fig. 3*C*, Part I, which will show them the curious head of *Daceton armigerum*, a Brazilian ant. In Chapter II, of Part I, we described the curious double mandibles of *Acanthognathus ocellatus*, and told how Möller, while in Sta. Catharina in Brazil, proved that the short basal pair was used for transporting the brood and grains of sand, while the long, narrow terminal pair serves only for biting enemies, and probably causes the ant itself to leap backwards in the act. According to Mayr and Wheeler, *Strumigenys saliens* and other *Strumigenys*, as well as *Daceton*, leap in similar fashion with their long mandibles, the only ones possessed by these genera. The genus *Strumigenys*, moreover, has in its sub-genus *Cephaloxys* a complete range of transitions between the long mandibles seen in our illustrations and short mandibles furnished with a dentated terminal edge.

Wheeler thinks that various species of *Strumigenys* live in lestobiosis with other ants under stones. It is possible that they use their long mandibles to catch the brood of these other species. Many *Strumigenys*, moreover, possess hairs terminated by clubs which are often shiny, as we saw at the end of Chapter III in Part I. Hairs of a similar character are transformed in certain *Cryptocerus* into gold or silver scales.

On the dome of an *Atta* nest in a piece of decayed wood in the virgin forest of Colombia, at the foot of the Sierra Nevada of Santa Marta, I myself found the race *spei* of *Rhopalothrix Simoni*, but I had no time to observe its habits. *Rhopalothrix* has ordinary broad triangular and dentated mandibles.

To sum up, we have in the *Rhagomyrmicinæ* a vast field for biological observations on habits, by future experimenters; this is a hint to those who live in tropical and subtropical countries.

Chapter VII

DIVERSA

In this chapter I should like to combine a number of facts which are too disconnected and diverse to deserve a separate chapter for each, but which should not be omitted. They may be grouped under sub-headings.

1 The Ponerinæ

We saw in Chapters I and V of Part I that the *Ponerinæ* are by their phylogeny the most primitive of ants, the descendants of an unknown 'pre-ant' which must have existed in the earliest geological periods. And this is proved more and more by observation of their habits.

Fig. 1*A* is an illustration of their mobile larvæ, which are very independent and have mouths supplied with serviceable jaws. Compared with those of the other sub-families in *B* and *C* of the same figure, it looks almost like some fierce animal by the side of children in swaddling-clothes, and Wheeler has actually proved that it devours unaided the dead or motionless prey which the ☿ or ♀ place at its disposal. This seems to be the case with all the *Ponerinæ*; so far as I am aware, no exception has hitherto been found. Even the larvæ of the *Dorylinæ* (*Eciton* and *Anomma*) which I have had an opportunity of seeing are much less nimble and more dependent upon the ☿ than those of the *Ponerinæ*, which are furthermore able to open their cocoons and come out of their

nymph-skins, and thus hatch entirely on their own account. The ♀ and ♂ are equally capable.

The exchange of social service, mutual understanding and antennal language are much less highly developed in general in the *Ponerinæ* than in the other sub-families. Their activity is much more individual. Except in the case of certain termite-hunts conducted by *Ophthalmopone*, *Lobopelta*, etc., and observed by Ilg, Wroughton and others, the *Ponerinæ* have rarely been seen to act in concert, carry one another about and come to a speedy understanding with one another, as do the *Dorylinæ*, whose habits were described in Chapter I. The partial exceptions I have just mentioned, however, prove that certain genera, especially *Leptogenys* (*Lobopelta*), *Diacamma*, *Megaloponera* and *Ophthalmopone*, possess the definite foundations of those remarkable social instincts possessed by the other sub-families. Among other matters I may refer to the mutual toilet operations carried out by the *Diacamma* ☿ (Part III, Chapter III, 5).

No genus of *Ponerinæ* is capable of weaving, or of making earth-masonry or carton-nests; I do not know of any which even bore galleries in wood. All *Ponerinæ* nests which I have had a chance of seeing were simply mined in the earth or in decayed wood, without even possessing craters. Some species live in dry, hollow stems—*Neoponera stipitum*, for example, which I discovered under these circumstances in Colombia.

To my knowledge, no genus of *Ponerinæ* is able to rear aphids or coccids, or any other cattle. Ant-gardens are as completely unknown to them as fungus-gardens or seed-harvesting.

Negations therefore abound; but we do know that the powerful sting and strong mandibles of the *Ponerinæ* make them formidable enemies, especially to the termites; and in

spite of all, they invariably live in society, however old-fashioned and simple it may be.

For precise observations of the *Ponerinæ*, we are chiefly indebted to Wheeler. He has observed among other things the way in which *Pachycondyla*, *Lobopelta* and *Odontomachus* in an apparatus bring their larvæ insects which they themselves have cut into pieces, and watch the young creatures devour their prey. When one larvæ has nearly finished its meal, the piece of insect is carried to another, and so forth.

Wheeler tells us that in the antique fauna of Australia the *Ponerinæ* are dominant. Among them is the large and terrible genus *Myrmecia*, which, together with *Amblyopone*, *Mystrium* and *Cerapachys*, is certainly one of the most primitive ant-genera. Plate XVI represents (*a*) the curious genus *Mystrium*. The genera *Myrmecia* and *Phyracaces* are depicted in our Plate I of Volume I. *Phyracaces* is closely akin to *Cerapachys;* its name being merely a transposition of the letters in the word *Cerapachys*. Topper observed the nuptial flight of the ♀ and ♂ *Myrmecia*, which flew about his head in hundreds and covered the bushes in the neighbourhood with their pairs. All the *Ponerinæ* except *Myrmecia*, certain *Lobopelta* and a few *Odontomachini*, form small colonies, often consisting of thirty to a hundred individuals only. The ☿ are all alike in shape and almost so in size, being just a little smaller than the ♀ and a little larger than the ♂.

Neither Wheeler nor I have ever seen the *Ponerinæ* regurgitate food to one another, in the manner of the two *Camponotus* depicted on our cover, though Cook declares that he has seen something of a similar character in *Ectatomma tuberculatum* of America. All the *Ponerinæ* feed on insects, but some of them have specialized tastes; certain genera delight in termites, as we read in Part IV,

Chapter IV, on the authority of Ilg, while others prefer millipedes, etc.

The foundation of formicaries apparently takes place in the same way as with other ants, and is the work of isolated females; at any rate, so we must needs judge from certain careful observations of Wheeler's upon *Odontomachus clarus* in Texas, etc.

In short, as I showed as early as 1903, in the *Annals of the Belgian Entomological Society*, p. 251, the *Dorylinæ* are only an offshoot of the tribe of *Cerapachysini*, or primitive *Ponerinæ*, which has become nomadic. They can no longer be considered, according to Emery's old idea, as the most primitive stock of ants. Each of the other sub-families is directly descended from the *Ponerinæ;* of that there can be no doubt whatever.

With this and my remarks in Chapter I, I conclude all I have to say as to the habits of the two first sub-families of ants, the *Ponerinæ* and *Dorylinæ*.

2 The Pseudomyrmini

On the basis of his studies of the gizzard and the larvæ of ants, and also of their nutrition, as quoted at the end of Chapter V in Part III, Wheeler has thought fit to set up two new sub-families from the two tribes, the *Cerapachysini*, an offshoot of the *Ponerinæ*, and the *Pseudomyrmini*, an offshoot of the *Myrmicinæ*. Emery and I considered that the question had not yet been thrashed out to a sufficient extent to justify such an innovation.

Nevertheless, I must refer to the peculiarities of the *Pseudomyrmini* larvæ, such as their special gullet or *Trophothylax* with its food-pellet, and their stridulatory apparatus or *Trophorhinium* (Part III, Chapter V).

However that may be, there can be no question that the

section I have entitled *Promyrmicinæ*, including its tribes the *Pseudomyrmini* and *Metaponini*, constitutes the primitive stock of the *Myrmicinæ*. As yet we know scarcely anything of the mode of life adopted by the *Metaponini*. *Metapone Greeni* was found by Green in the galleries of a dead tree-branch in Ceylon, together with some termites, which it probably used as food. The habits of *Pseudomyrma*, on the other hand, are fairly well known.

In Part III, Chapter III, I mentioned the provision made by certain ants for the exchange of food with one another, by means of nurses, or with their larvæ. In the latter case, *Pædalgus* and *Pachysima* are characteristic genera, *Pachysima* being a member of the *Pseudomyrmini*. To this I may add that the trophothylax of *Pseudomyrma* sometimes contains not only insect-débris, but pollen from flowers and those bodies known as Belt-corpuscles, which come from the extra-floral nectaries of plants, so called because they supply nectar like honey or sugar on the leaves or stems of plants and therefore outside the flowers. Thus the *Pseudomyrmini* and their larvæ are no longer essentially carnivorous, like the *Ponerinæ*, but omnivorous. In fact, as we saw in Chapter II, according to Horne *Sima rufonigra* of India even stores seeds like *Messor*. *Sima* and the *Pachysima* are the *Pseudomyrmini* of the Old Continent.

P. elongata, a species of *Pseudomyrma*, digs its nest in the earth, and I myself have found it in this situation. All the others nest in dry, hollow stems, in the manner described in Part II, Chapter VI, or in the hollow stems of living trees, as I explained in Chapter III of the same part. Specially remarkable cases of this occur in *Pseudomyrma* of the *Triplaris*, and also in *Pseudomyrma* of the *Cordia* and *Tachigalia*, and in those living in acacia-spines. All these *Pseudomyrma* use their powerful stings, which have a very

painful effect, to defend the plant wherein they nest from the attacks of all other creatures, including the leaf-cutting *Atta* and *Acromyrmex*. It matters very little whether this is a case of special *adaptation* by partial *symbiosis* between plant and ant, or merely a chance phenomenon; nothing alters the fact.

Other *Pseudomyrma*, such as *P. Küncheli*, live in the dry branches of trees and have an equally terrible bite, of which I have had personal experience. On the trees of tropical America, the *Pseudomyrma* are in every respect the rivals of *Azteca*.

The habits of the *Sima* and *Pachysima* of Asia and Africa are still very little known, but the narrow elongated and compressed form of their bodies points to the belief that they generally live in a manner similar to that of *Pseudomyrma*.

The ♀ of the *Pseudomyrmini* usually have heads and abdomens quite disproportionately long and narrow, much more so than those of their ☿, which are always monomorphous and equal in size in every species. The exceptions, such as *Sima rufonigra*, which is a harvester and lives in the ground, only confirm the rule. The ☿ of *Pseudomyrma filiformis* is absurdly narrow, and the ♀ has a long head with parallel edges; in brief, everything suggests that these insects usually live in narrow stems, like the cases cited above and dealt with in Part II. Seeing that the ♀ is larger than the other sexes, if she is to live in the same stems as they her body must certainly elongate still more in proportion. Thus once again, dear reader, you see how the phylogeny of a creature's body gradually adapts itself to that of its habits.

3 The Cremastogastrini

Here we have a very compact group, distributed throughout the world, except for the Northern Alps and the

Himalayas, and also the Antarctic fauna properly so-called. Figs. 99 and 100 (Part IV) show the typical form and motion of *Cremastogaster* and its sub-genera. The heart-shaped abdomen tapers towards its extremity and can be folded back over the thorax, even over the head. The two nodes of the pedicel are flattened from top to bottom in order to help in the upraising of the abdomen. Its point is also very mobile, so that it may sprinkle the ant's poison right and left upon any enemy that appears.

The *Cremastogastrini* ☿ are monomorphous, but nevertheless they are pure *Myrmicinæ*. Many of them make charming carton-nests on trees, such as those depicted in Plates V and VI; most of them rear aphids as cattle. In Part IV, Chapter V, we discussed the parabiosis of certain *Cremastogaster* with other ants, and this need not be dealt with again.

It is extraordinarily amusing to observe *Cremastogaster* ☿ filing out to milk their aphids and returning. At the slightest alarm, these ☿ wheel their bodies round with their abdomens upraised, especially when their crop is empty. We have seen how the African *Cremastogaster* which live in *Acacia* spines defend themselves from the raids of the *Anomma* by placing the points of their abdomens together near the opening of the spine in order to sprinkle the aggressors with poisons. In Part II, Chapter IV, we also saw how that astute little humbug of a mosquito, *Harpagomyia splendens* depicted in Plate XIV deceives the worthy *Cremastogaster* (*Physocrema*) *deformis* and swallows a drop of her honey-dew. The *Physocrema* instinctively regurgitates to the thief when it tickles her in an agreeable manner with its antennæ.

The reason for the broad and swollen epinotum of the sub-genus *Physocrema* is a rather interesting problem which has been solved by Smith and Bingham. These authors

have proved that in *Physocrema inflata* and *deformis* of India a sweet liquid is exuded through an orifice in this epinotum and licked up by other ☿. This, I presume, is a special secretion from the metathoracic gland, the equivalent of which will certainly be found in the American species *arcuata* and *Montezumia*.

Another curious sub-genus is *Oxygyna*, whose tiny ♀ are sometimes scarcely larger than the ☿, and have curved and pointed mandibles very similar to those of *Polyergus*, represented in Plate III 3, *o*, (Volume I) and fig. 106 (Part IV). The ♀, on the other hand, have the ordinary dentated and triangular mandibles. As to the reason for this peculiarity in the *Oxygyna* ♀, we have at present, unfortunately, no experimental proof, but it seems as though the analogy between this creature's habits and those of the small parasitic ♀ of the genus *Formica*, described in Chapter II, *b*, of Part III, would be as striking as that between its mandibles and those of the *Polyergus* and *Strongylognathus* ☿ and ♀. Hence I offer the following suppositions, to which Wheeler assents:

a That the *Oxygyna* ♀ are the parasites of other ants, probably other *Cremastogaster*, just as the *Formica difficilis*, *microgyna*, etc., are the parasites of *Serviformica*.

b That their mandibles are probably used to pierce the head of the ♀ whose nest they have invaded, after being adopted by the ☿, or possibly by the colony-queen herself, whom they proceed to kill.

c That this is most probably, therefore, a case of temporary parasitism on the part of the idle ♀, whose hard-working progeny afterwards replaces that of the queen of another species—an insect capable of founding a formicary on her own account, as the little *Oxygyna* ♀ is apparently incapable of doing.

Doubtless our successors will find out whether this is correct or not.

The sub-genus *Decacrema* is very common in Borneo. In this island Haviland found several races of *D. borneensis* on the tree known as *Macaranga*, living in symbiosis with it. The ♀ of the sub-genus *Atopogyna* have long mandibles, pointed but triangular, dentated and crossed, especially in *A. depressa;* their special function is as yet unknown.

4 The Genus Pheidole

The enormous genus *Pheidole* has exactly the same geographical distribution as the *Cremastogastrini*, but is distinguished from them by the extreme polymorphism of its ☿, and its transition to other groups by way of kindred genera such as *Ischnomyrmex*, *Ceratopheidole*, *Parapheidole*, *Novomessor*, etc. Between the giant ☿ and the small ☿ of these kindred genera comes a medium-sized form, as in certain sub-genera of *Pheidole*, such as *Anisopheidole* and *Elasmopheidole*. The true *Pheidole* has a distinct ♃, without any transitional forms, entirely separate from the worker. By way of the genus *Pheidologeton*, represented in Plate III, *a*, *b* and *c* (Volume I), the tribe of *Pheidologetini* shows a striking analogy with *Pheidole*, while on the other hand it has gradations to the *Solenopsidini* by way of *Oligomyrmex* and *Aëromyrma*, whose worker is also polymorphic.

Close to *Pheidole* we must place its parasites, the genera *Epipheidole* and *Sympheidole*, to which we alluded under headings 13 and 14 in Chapter VII, Part III.

Fig. 3*D*, p. 42 (Volume I), shows the elongated head of the ♃ in *Ph. lamia*. This head is sometimes longer and often wider than all the rest of the body.

In Chapter II we saw that *Pheidole* is sometimes a harvester, especially in India. But this is by no means invariably

the case. *Pheidole Bergi* of the Argentine, whose crater is shown in fig. 45*A* (Volume I), digs underneath this crater a deep passage whose subterranean chambers never contain seeds, but only the fragmentary remains of insects killed by this ant, as Dr. Bruch has proved.

Other *Pheidole*, such as *Ph. Sykesi*, are exclusively granivorous, but most of them—the European *Ph. pallidula* and the cosmopolite *megacephala*, for example—are omnivorous, varying their diet according to place and circumstance.

The geographical distribution of *Pheidole* is identical with that of the *Cremastogastrini*. These two groups appear and disappear in the same countries or regions, in spite of the difference in their way of living. But *Pheidole* is an earth-loving ant ; I have never seen her in a nest that is either woven, or sculptured in wood, or made of carton. She digs in the ground, constructs masonry and sometimes builds circumvallations (*Sykesi*, *præusta*, *vallifica*) or lives in the cracks of rocks (*pallidula*).

5 Tree Ants

Practically all we need attempt here is a recapitulation. We have seen how a large and varied assortment of ants nest in trees, sometimes simply under the trunks, in and under the bark of the branches and even the twigs, in hollows which are either natural or the result of approaching decay, or formed by artificial means, and sometimes in carton nests which they have constructed with a greater or less degree of art. We know that these nests, like the woven nests, are usually kept close against the trunks, branches, twigs or even the leaves of many trees and bushes (*Polyrhachis*, *Camponotus*, *Dolichoderus*, *Tetramorium*, etc.) or maybe built between two of them. We have found that many

places which can be excavated, such as insect-galls and other injurious or natural excrescences of certain plants, their spines, the undersides of the leaves of climbing plants, even the space between two sides of a leaf that has been gnawed by a little grub, are used as nests by various ants. We have discussed the ant-gardens constructed on trees in flooded tropical regions by means of epiphytes of parasitic plants, and the way in which certain ants such as *Azteca* and *Pseudomyrma*, in tropical America, reign like queens, strong to defend, over the magnificent virgin forest and all the hosts of enemies that attack it, the worst of all being the *Attini*. Is this all ?

We are scarcely in a position to tell what happens within the heart of the thicket, or, more especially, on the forest tree-tops where birds and monkeys rival the ants. We are too heavy and earthy for that. It may be that our aviators will some day find a way of perching down on the trees of the virgin forest. When this happens, but not until then, I should like to be resuscitated, and become an aviator myself, for the sake of studying how my little friends live up in those heights.

As we wait for this paradise of the future, ants with gigantic eyes sometimes fall to the ground from the tree-tops and give us a glimpse of what their still unknown habits must be like.

This was the case, apparently, with *Gigantiops* of Brazil, which, according to Albert Schulz, can leap from one leaf to the other. Very little is known about the habits of the Australian *Opisthopsis*. According to Mjöberg, *O. Haddoni* nests in termite-galleries and *rufithorax* between the roots of trees, in spite of the enormous eyes of both. On the other hand, Mjöberg discovered the huge *Myrmecia Mjöbergi* living at a great height in the trees of the thick

Queensland forests, in the heads of epiphytes of the genus *Platycerium*.

In 1916 the Jesuit Father Kohl discovered in the Congo forests some specimens of a curious ☿ ant, completely antediluvian in character. Its eyes were enormous, and its gizzard, etc., proved it to be a co-representative with *Myrmoteras* of one of the most primitive forms of the *Formicinæ*. Its name is *Santschiella Kohli*. Its eyes covered nearly half the surface of its head, and it must have fallen from one of the trees in the forest.

Dendromyrmex of the tropical American forest, with its great convex eyes and its carton nests on the branches, is also a tree-haunting ant and a companion of the carton-making *Azteca*.

6 Ants of the Deserts and the Steppes

Here again, we must recapitulate. Fig. II (Volume I), depicted the psammophores (macrochætes) which are so characteristic of most desert ants, and in Part III, Chapter IV (4), we explained how they are utilized by these insects to lift and carry the sand. We also showed that several species of desert ants have a hollow on the underside of their heads, for the same purpose.

In Chapter II, as well as in Chapter VI (*A*2) of Part II, we described the deep granaries hollowed out by *Messor arenarius* in the Sahara, and also those made by *Pogonomyrmex* in the American plains.

In Chapter III (7) of Part III, we discussed the nurses which are represented in fig. 80, 81, and 82. These nurses are especially common in the steppes of Australia and America, where, as we have seen, they are used as reserve water-bottles during the dry season.

Such are the most distinctive and general characters of the

ants found in the deserts and steppes. They are very distinct adaptations to an environment in which water and vegetation are rare and poor, and in which heat and drought are the determining factors. It is interesting to find that the most dissimilar genera, *Camponotus* (*Myrmopsamma*), *Messor*, *Melophorus*, *Dorymyrmex*, etc., are able to adapt some of their species to the desert, some to the steppe or prairie, and some even to the forest (*Camponotus*).

Between the forest and the desert, we have all conceivable transitions—clearings, meadows, mountains of a more or less rocky character, and steppes. The ant fauna adapts itself to all these environments, to their moderate or extreme temperatures as well as their degree of humidity. We have made the acquaintances of ant-species which are extraordinarily adaptable, such as *Tetramorium cæspitum*, which sometimes lives in the Swiss meadows and in Norway, sometimes in the African steppes and sometimes even in city streets. But we have also made the acquaintance of purely local species, exclusively adapted to a very restricted environment, like *Messor caviceps* of the desert, and *Holcomyrmex Lameerei* (Chapter II) which rides astride her seed like a witch on her broom.

At all times and in all places, dear reader, there are evolutional transitions!

7 Agile Ants and Sluggish Ants

Chapter VII (1) of Part IV, showed the advantage gained by *R. sanguinea* over the slow *F. pratensis* by reason of her nimbler and quicker tactics, and under the second heading of the same chapter we gave an exact estimation of the speed of a marching *Polyergus rufescens* army. But these speeds are only moderate; there are an infinite number of variations above and below them. Extraordinarily rapid as the march

of a *Polyergus* army appears to us, we can yet easily distinguish every ☿ in its ranks.

But what shall we say of *Iridomyrmex analis* of the United States, *Prenolepis longicornis*, *Machæromyrma bombycina* of the Biskra dunes, even of our own *Serviformica picea*, all of which flash past like so many flying arrows, until no bodies can be seen, but only one line darting along like lightning! Their speed is truly phenomenal; I have never been able to measure it, but it must amount to nearly 50 cm. a second. How these feeble little creatures, excessively thin but very long-legged, and easily killed by the slightest pressure, can muster up enough strength to keep running at a prodigious speed which outwits all their enemies, seems an almost insoluble problem. But beyond all doubt, this extraordinary speed is their strength, and the means by which the cosmopolitan *Plagiolepis longipes* and *Prenolepis longicornis*, as well as *Iridomyrmex humilis*, have been able to swarm as they do in defiance of all other insects and of man, without the aid of wings.

The agile ants mine their nests in the earth or sand, or else take up their abode in the cracks of walls or rocks, where their brood is safe, and whence they can slip out and pilfer from our gardens and kitchens, carry off small corpses and even attack small insects.

At the other extreme, we have the sluggish ants. All ants, it is true, move more slowly under the influence of cold; but when they are weakened in this way they retire to their nests. Here I am speaking of those ants whose motions are always slow, even in warm weather. They put their trust in their hard chitinous armour, and are rarely aggressive, though we have mentioned a case in which *Cephalotes atratus* attacked a wasps' nest. As a rule they feign death when interfered with, and sometimes roll up into balls like hedgehogs or

porcupines: *Echinopla* and *Meranoplus* of India and Australia, for instance, behave in this way.

We have already mentioned our sluggish and peacefully-disposed *Myrmecina graminicola* of Europe, and its habits. But the slowest ants I have observed are *Sysphincta* and *Proceratium*. When one raises the stone or damp wood under which they shelter, these lethargic creatures make no attempt to run away, and scarcely even move. They merely contract their legs to a certain extent, like certain beetles, and remain motionless in other respects. I assume that the African *Melissotarsus* (fig. 87, Vol. I) must behave in a similar manner. The habits of the sluggish ants, except *Myrmecina*, have received very little study.

8 Jumping and Projecting Ants

In Chapter III of Part I we described the mandibles of various forward and backward leaping ants. The latter are represented in fig. 3*C* and *E* (Volume 1) and in Plate XVI in this volume. Plate XIV *K* shows the curious mandibles of the only jumping ants which have fully justified their claim to the title. They all belong to the genus *Harpegnathus*. Wroughton, who observed them in India, assured me in writing that he had seen *H. cruentatus* making spontaneous bounds half a metre long and more, like grasshoppers. But it does this by bending its head underneath its thorax and jerking it sharply upwards again. Plate XIV *K* will make this matter instantaneously clear. The sting of *Harpegnathus* is also cruel. According to Lowne and Froggatt, *Myrmecia nigrocincta* of Australia can leap 3 decimetres, but these authors do not say how it does so, whether with its head or its back legs.

According to Wheeler (1922) all the ☿ of *Pristomyrmecia*,

a sub-genus of the Australian *Myrmecia*, and also *Myrmecia pilosula* and *nigrocincta* take forward leaps an inch or several inches long, when they are disturbed, like Lilliputian cavalry on the gallop. *All these leaping species have thighs swollen at the lower end. Gigantiops* exemplifies this peculiarity (see below) but the non-leaping *Myrmecia* (*sanguinea*, etc.) do not. It is obvious, therefore, that they leap by means of their thighs, as grasshoppers do. Wheeler makes this fact the basis of a new sub-genus *Halmamyrmecia*, including *M. pilosula* and *nigrocincta*.

Bingham says that *Harpegnathus* and *Odontomachus* leap forward and backward only when frightened or disturbed; otherwise they walk like other ants.

As we said before, the backward-leaping or 'Tak' ants act in a different way. Picture to yourself, dear reader, the closed mandibles of *Odontomachus*, shown in fig. 3*E* of our first Volume. These mandibles are open at their extremity, and they are separated in such a way as to form a single line perpendicular with the sides of the head, that is, precisely continuing its anterior edge on either side. This is the ant's position of defence, adopted when it is protecting its doorway, for example, as in the case of the *Colobopsis* ♀ or the large *Atta* ☿. Then imagine that an object is thrust towards these open mandibles. Suddenly they close, striking the object without gripping it. At the same moment the ant leaps several centimetres backward, emitting a slight sound, a distinctly perceptible 'tic.' In doing this, the sole object of *Odontomachus* is to frighten the intruder or enemy, and not to bite severely. Two or three inward-curving teeth at the end of the mandibles are relatively sharp, according to species. They are also evidently used to carry the brood, etc., and to bite in good earnest when necessary. According to Schupp, an *Odontomachus* head

that has just been separated from the rest of the body is still capable of leaping backward.

Hetschko and Mayr tell us that the *Dacetini* tribe of the *Rhagomyrmicinæ* (Chapter VI) has one species, *Strumigenys saliens*, which leaps in exactly the same way as *Odontomachus*. According to Mayr and Möller, *Acanthognathus* does the same. I do not think I shall be far wrong if I attribute the same faculty to the *Dacetini* in general, when they feel they are in danger.

Finally, I will recall what we said above under No. 5 while dealing with the Tree Ants, about Schulz's account of *Gigantiops destructor*. In spite of their long legs and the distinctly swollen hind half possessed by this huge-eyed ant, Schulz's observation requires confirmation. We do not know by what means *Gigantiops*, which lives in the Brazilian forests, manages to leap from one leaf to another. It may do so in the manner of the grasshopper, by folding up its back legs, leaning upon its tibiæ and tarsi, and making the muscles of its swollen thighs play upon them. But here again we must wait, and not judge prematurely. In any case, the long back legs of *Gigantiops* are not without their points of resemblance to those of the grasshopper.

After writing the above, I received from my colleague, W. M. Wheeler, certain personal observations which he himself had made at Kartabo, British Guiana—in 1921, I believe. They are enshrined in the *Biological Bulletin*, Vol. XLII, No. 4, April 1922 (Obs. on *Gigantiops destructor* F. etc.) and they make the matter clear.

Wheeler and his son discovered two *Gigantiops* nests lying on the leaves between the nodes of Cecropias which had fallen to the ground and decayed. Their formicaries were small, comprising only 50–60 ☿, and the larvæ were cocoon-spinners. Mann also recently found a *Gigantiops* nest in

Bolivia under the stones on the ground. It is therefore not an inhabitant of the trees, as was hitherto supposed.

When a *Gigantiops* is pursued, Wheeler tells us, it jumps forward to a distance of several inches, with a graceful movement like that of a cat. Wheeler thinks that in order to do this it utilizes the swollen lower half of its thighs, grasshopper fashion, as I said above. *Gigantiops* jumps from leaf to leaf on bushes in a similar way.

Gigantiops shows a striking mimicry of *Neoponera apicalis*. Wheeler has seen these ants carrying termites between their mandibles.

With this account of jumping and projecting ants, we finally take leave of the specialized habits of our friends, and project ourselves into the Epilogue. I have designed this Epilogue to compare their lives with that of other live creatures in the realm of nature, especially with that of the termites and with our own human society.

Epilogue

1 What is a Living Creature?

To the little world of the microscope we give the name of microcosm. It is supposed that the microcosm of living creatures has been engendered by the chemical and physical atoms of a lifeless substance which we describe as amorphous or inert, though it often moves a great deal, as wind, fire, and electricity prove to us, for example, and though it sometimes possesses distinct forms for every chemical combination, as in the case of crystals.

The first characteristics which distinguishes live creatures from lifeless things is this: each of them belongs to a species, more or less distinct from thousands of other species—that is, from what we call the individuals of every species, the duration of whose 'life' may vary from a few hours to a few

hundred years. These individuals have the faculty of almost exactly reproducing the life of their ancestors, with all their complicated characters, by means of a single microscopic 'cell.' The faculty in question is called heredity. The slow transformation of the living species themselves in the course of millions of years we call phylogeny and the progressive transformation of every living individual, from the cell which gave rise to it, we call ontogeny. This transformation takes place either by a simple process of sub-division or by germination. In complicated beings, composed of a number of cells throughout childhood and the adult stage, until death, it takes place by germination. We have discussed the phylogeny and ontogenesis of ants in Chapters I and II of Part I.

There are, then, three fundamental facts which characterize all things that are alive and distinguish them from all that is lifeless.

1 Each of them consists of a cell or number of cells.

2 They all reproduce their species, either by a simple process of cell-division, when only one cell is present, or by the budding of a group of cells, or by germination, that is by means of one or two special cells described as genital, which have the capacity of reproducing all the individual phases of life in their species. The genital cells must therefore contain in latent potential form all the present and future hereditary characteristics of the individual to which they give rise. If germination takes place from a single ♀ cell, it is called parthenogenesis, but if it can only take place through the combination of the ♀ nucleus with that of another cell denoted by ♂, it is called sexual reproduction. The second condition is the invariable rule in man, but not in ants. In the case of the living creatures which we call primitive, and which consist of a single cell (microbes, for

a. *Mystrium Voeltzkowi* ♀ Madagascar.

b. *Melophorus Wheeleri* ♀. Australia.

c. *Orectognathus sexspinosus* ♀. Australia.

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c. Ornithogalum arcuatum ♀. Asparagi.

d. Muscari botryoides ♀. Asparagi.

e. Muscari racemosum ♀. Asparagi.

example) it sometimes happens that two cells meet each other by chance, and each exchanges half its nucleus with the other; this process takes the place of sexual reproduction by the ♂ and ♀ cells of more complicated beings.

3 Hence the fact of specific heredity, which is proper to all living things, is the fundamental fact distinguishing them from all lifeless things. So long as we are unable to manufacture by artificial means a living cell with all its specific heredity, every hypothetical attempt to derive life from amorphous or inert atoms is doomed to failure, like the idle discussions between 'vitalists' and 'mechanists,' each of whom imagines that he can explain life in his own way. Here, as before, we must learn to hold our peace and wait.

The whole problem of life, therefore, depends on that of the living cell, which people such as Hæckel once imagined to be very simple. This was a fundamental error. But since then our scientific conceptions have changed. When I was studying at Lausanne, between 1862 and 1868, nothing about the evolution of living creatures was as yet being taught, and Cuvier's theory of deluges, which were supposed to have destroyed all life on earth in successive catastrophes that God might create it anew, was not yet discountenanced in the schools. In physics and chemistry, moreover, our teachers at college still told us in all good faith that lifeless substance consisted of two distinct units, the indivisible atom and the molecule formed in various ways by congregations of atoms. I must own that I never succeeded at the time in getting the dogma of the indivisible atom into my head. In fact, no sooner had I the engraphic image of such an atom than I could see it cut in two or four again by the ecphory of my inductive logic, in face of which the notion of indivisibility remained as unintelligible as Chinese.

Soon, however, I read Darwin's *Origin of Species*, and his

proof of the slow evolution of living creatures by phylogeny delivered me from the nightmare of successive deluges. Then came the discovery of radium, which freed me from my other nightmare, the indivisibility of material atoms. Our modern ions and electrons now dance in infinitely divisible 'matter' and in an equally metaphysical 'infinity.' In other words, this infinity is no less incomprehensible or immeasureable for our brains than the essence of matter itself, or than all that we imagine under the 'infinitely' diluted terms of our abstractions—which therefore claim to be 'absolute'—'God,' ' Universe,' 'Soul independent of the living body,' etc., etc., Amen!

After this humble confession of our ignorance, made not to a priest, a mere human being like the rest of us, but to ourselves—let us return to known facts and begin with the cell. Glance, friend reader, at the cell represented in fig. 17 (Part I). It is bathed in the white blood of the ant, and receives oxygen from the air through four small tracheæ. From these two things its protoplasm elaborates a complicated chemical poison, eliminating by way of the kidneys (Malpighian vessels) all the useless refuse of its chemical activities. We have seen how the *Dolichoderinæ* use this poison, the product of their anal glands.

Now this single cell, dear reader, reveals a number of things to us:

In the first place, present-day research is proving to us more and more that, however microscopic the cell may seem to us, it is a little world of infinite complexity. In its own way this little world has almost as many varied complications to show us as the different animal species and multicellular plants (those composed of many cells) exemplified so often by the ants about which we have been reading. Consider the significance of the infinitely large and infinitely small.

Compare the systems of stars and countless suns with our puny globe, which seems to us so huge—in spite of Jules Verne's 80 days, now reduced to 30. Then compare our self-styled human greatness with that of the ant and the cell. All then is relative. And now that science has rejected the indivisible atom, imagine the cell as a great world, a monster which has gradually attained to a state of extreme complexity at the expense of all kinds of organs, which the increasing power of our strongest microscopes, and even our ultra-microscopes, cannot reach.

Lastly, read or re-read Voltaire's famous *Micromegas*. Thus will your aspirations become more modest, and you will learn to bow the head before the Unknown and Infinite.

In the second place, you will now understand how the microscopic reproductive cell from which you yourself are born, the ovum of your mother combined with the spermatazoön of your father (see Part I) has actually managed to contain as latent (hidden) force all the hereditary dispositions, whether bodily or mental (*i.e.*, relating to the cerebral functions), that belong to your cherished self. These hereditary tendencies of your ontogeny have been accumulated in your phylogeny by all your human and animal ancestors for countless millions of years, lost in the darkness of time—a darkness which in its turn is infinite. The ontogeny of the individual is short, and can be observed in its entirety for each species. But the phylogeny of species is very slow in comparison with our short life. We can submit none of it to proof, therefore, except a few of its last branches.

These few first facts show you the absurdity of dogmas which speak of a 'simple cell' as the origin of life, descended from a simple solution of lime or some such substance, like Hæckel's famous monera. Nowadays we are forced to own that we know *absolutely nothing* about the origin of life, which

most probably took place or maybe is still taking place in a sub-cell or pre-cell much too microscopic to be within reach of our present means of investigation. However, the future still certainly has in store for us a number of surprises which no lame hypotheses have the right arrogantly to anticipate. It is claimed that the germs of life have been found embedded in meteorites from stars beyond this earth, and who shall say that this is not true?

In the third place, we must not forget that only the cells of unicellular creatures (those consisting of one cell), like microbes and amœbæ, and the reproductive cells, whether fertilized or not, belonging to all other living creatures, possess in potential form the entire hereditary make-up of the individual produced from them. The other, non-reproductive cells of multi-cellular creatures, at any rate those of the somewhat higher animals, such as ants, are incapable of reproducing the whole creature, whereas cuttings from plants can do so. Why should this be ? It is because in animals they have been differentiated more and more as various organs: muscles, nerves, special glands (as in fig. 13, Vol. I), kidneys, blood, skin, etc. The cells of these organs, being adapted to their special functions, have gradually lost the power of germinating, that is, reproducing the *whole* individual. But they have not therefore lost their hereditary peculiarities, since they reappear in every individual ontogeny with faithful reproduction of the form and function possessed by the corresponding cells of their parents and ancestors. It is by means of these specialized cells that every animal species reproduces the shape, hair, internal organs, colour and even movements of former generations with such minute exactitude. And it is by means of this exact reproduction that the natural history specialist can infallibly determine the species of a certain little ant,

for instance, which is sent to him from Australia, let us say, or Tonkin, or the Antilles.

The 'heredity' of specialized cells is reproduced, therefore, not by the cells themselves, but through the medium of germinative cells, which contain all their specialized peculiarities in latent potential form. For instance, the germinative cells of the fertilized ♀ ants contain all the peculiarities of the ☿ and ♃. We must admit, therefore, that heredity is a very complex thing, and so also is the cell. Countless ancestors are combined to infinity in the heredity of each of us. But so long as comparative fixed species have not yet been formed, and as the living being still belongs to a mere variety or race, cross-breeding between individuals of these diverse varieties or races will render their offspring unstable, a combination of these parent forms, though already divergent.

Ants, termites and men are all complicated living creatures, composed of very different organs with specialized cells. The sexual glands alone can reproduce the individual as a whole, though we have seen that ants are still able to do this by parthenogenesis. The various organs, in ourselves as well as in the ants, may be considered as a confederation of cells, directed by the brain to a greater or less extent according to the relative power of that organ. The relative independence of organs varies, the glands, for example, being more independent than the muscles; but generally speaking their confederation constitutes one whole, whose parts cannot live long without one another—in spite of the experiments quoted in Part II, Chapter II, dealing with ants whose heads were separated from the rest of their bodies. The cells of every organ in this confederation have been admirably adapted, through gradual hereditary phylogeny, to their function. Even when some of them eat

the others, as certain cellulophagous cells called 'phagocytes' eat the wing muscles of the fertilized ♀, or even when the mother eats her own eggs to feed her larvæ, it all takes place in a spirit of peace and amity. But where and how did this confederation of cells begin to form different organs?

The key to this riddle lies with certain so-called lower animals, the protozoa. They each consist of a single cell, but this cell can be diversified in several ways to form false feet or pseudopods, vibratory cilia and various complications. Infusoria, corals and various lower animals, however, form for the most part *associations of similar cells*. These associations are transformed into more intimate unions, and thus the creature becomes multicellular. The first common organ formed in this way is a kind of stomach, with a single opening, which serves both as a mouth and an anus. This stomach consists of two layers of cells, the *ectoderm* outside and the *entoderm* inside; the first covers the second, and becomes the skin; the second digests in common the cells which are swallowed, and afterwards rejects them through the mouth. Such is the formation of animals which constitute a transition between the protozoa and metazoa.

From this phylogenetic starting-point other associations of cells begin their work, the initiation of new organs, which are specialized as multicellular pseudopods, glands, the first smooth muscle fibres (consisting of scattered retractile hairs), the primitive neurones (consisting likewise of scattered gangliar cells), the mobile cells of the blood, and later the respiratory organs, the brain, a differentiated reproductive apparatus, etc. For instance, the association of cells in the polyps, sponges, etc., is not at first intimate in character. Any group which is formed among them suffices

to reproduce the whole collective 'individual' of the associated cells, by a simple bud or slip, somewhat as in the case of plants. But such a collective individual already has a specialized form as a member of a certain species, like each of the cells composing it.

How is it that a collection of cells with so little coherence can function in a co-ordinated manner? In plants, which do not move about, the circulation of the sap may suffice to achieve this purpose. But a living, mobile creature has need of some retractile apparatus enabling the whole organism to move, whereas a single cell merely requires vibratory cilia for its movements. The muscular fibres were specialized for a purpose such as this. However, before the movements of the various muscles could be co-ordinated, there had to be something to put them in communication with one another. Hence in due course the neurone was differentiated from the gangliar cell. Its rôle was to be sensitive to irritations received from without, and then to act on the muscles, the glands and its fellow-neurones. In this way, the cellular communities which constituted the primitive animal were enabled to function, though their power of motion was but slight.

Then came the gradual formation of the first nerve centres, known as ganglia, which were capable of dominating a republic of cells and bringing them to a higher condition of unity. At the same time the striated muscles were formed, and swifter motion became possible. The animal's strength, liveliness and motor independence increased. But as these ganglia multiplied in a single individual body, they in their turn were in need of a superior unity—a kind of monarchy; this was a growing necessity for such a coherent whole as the republic of cells in an animal individual was now becoming. Thus it was that the brain first originated,

and developed more and more in the exercise of its kingly function. Whether it arose from a single ganglion superimposed upon the others, as in the case of ants, or from many ganglia welded together, as in the spine of the vertebrates (fishes and reptiles) is of minor importance. It never becomes a 'roi fainéant' except in certain vile, degenerate parasites.

In the first place, however, the brain itself did nothing but give a vague general impulsion to the movements of the entire body, and turn them into some direction useful to it as a whole. The instinctive movements, especially those described as reflex, which are directed from the ganglia or the spine, still preserved a high degree of independence. It was only gradually, in the course of millions of years, that the brain-king acquired over the whole animal body a sway which became more and more autocratic, but at the same time more plastic and more adaptable to the external world. The body of a reptile or ant can live for several hours without a brain, but if a man is beheaded or deprived of his spine, he dies at once.

I have tried here, dear reader, to give you a rapid sketch of the development of animal life from its starting-point in the primitive cell, where it is still almost identical with the *primitive vegetable cell* which develops on its own account, in a somewhat different way, into associations of cells.

Furthermore, these separate mobile individuals of the multicellular animals have also at times a tendency to associate with each other as the cells of which they are composed were wont to do at first, but except in the case of the family, the close relationship between parents and their immediate offspring during childhood, such associations are exceptional. Living creatures use up the best of their vital strength in destroying and devouring one another. This is sad, but it cannot be denied! The communal life of our little

friends the ants and the termites is one praiseworthy exception. The present work has been devoted to an account of its peculiarities, and we shall return to the subject in a moment. In this case, however, the brain-kings are separated from one another and move about separately. For this reason, in ants as in men, the *species* has ceased to be the determining factor in association. Thus we have seen how ants of the same species, even the daughters of one mother, will fight each other to the death, and yet live all the while in communal association with different species and even different sub-families, not to mention other insects, as we live with our dogs or horses.

In the introduction to Part I, and in Chapter II of Part II, we explained in a few words the significance of the terms used by Semon in his Mneme—engram, ecphory, etc. I should like here to emphasize once more that these terms refer to living creatures *only*, but that they are equally applicable to phylogeny (inherited characters) and ontogeny (characters acquired during the individual unicellular or multicellular life, including memory). All this, then, remains entirely within the domain of positive scientific knowledge, which we can explore by means of our senses and our brain.

And now we come to the counterpart, and face the question; how much is there that we do not know in connection with the alleged mechanical origin of living creatures? This I shall answer briefly. We do not know:

(1) The nature of the ultra-microscopic sub-cell in which the source of heredity was formed; (2) the way in which mnemic engraphy, acting continually throughout ontogeny, was able to produce in the dark night of time, through the heredity of characters thus acquired, that evolutionary phylogeny which insensibly transforms species by way of

their genital cells—in short, how the heredity of acquired characters is mechanically *manufactured;* (3) the metaphysics of our self-consciousness (Bewusstsein), that is, the intimate connection between the functions of our brain and the mirror of our mind, by way of the introspection of our sensations and representations, compared one with another by means of our movements; the third of these unsolved mysteries has been styled psycho-physiology. The absolute mutual dependence of the active functions of our major brain, and the knowledge of our ego (our mind) is definitely proved by scientific facts; but their essential identity remains, for us, a question of metaphysics—and therefore unknowable.

From this brief survey it follows that our scientific inductions, which we call *objective*, are not really based on the ultimate *nature* or essence of the objects in question—for this, now and forever, will be beyond our knowledge—but exclusively upon the *subjective* introspection provided by our sensations, perceptions, representations (ecphories subtilized by means of language, which is all too often deceptive). Hence all that we consider to be objective and scientifically proven is really only a result laboriously acquired by the primitive sensations with which our sense-organs have furnished us. By repeating these, transforming them into perceptions and comparing them with one another through the agency of our movements, we succeed not only in proving that nature and various objects exist outside ourselves, but in learning to know these objects in ever greater detail. Instruments of precision, such as weights, measures, watches, microscopes, telescopes and mathematical figures help us to do this.

That is why Sganarelle in Molière's *Mariage forcé* won his argument with the metaphysician Marphurius, and proved it

to him in a manner both scientific and practical, by showering blows upon him with a stick. It is not merely a supposition that the external natural world exists outside our individual consciousness; it has a very real existence. We know what it betrays to our senses, but we only know it through their medium, and are ignorant of its essence. For instance, to cite just one case, we have no special electrical sense, and we only know what electricity betrays to our senses and our composite scientific instruments. This is true not only for us but also for fairly complex animals endowed with brains—and therefore it is true for the minds of ants. Their senses, especially that of smell, certainly differ somewhat from our own, as our scientific inductive investigations have enabled us to realize (Part II, Chapter I). But though we can obtain no absolute knowledge of what is going on in their minds, neither can we see what is going on in the minds of our human neighbours. And can it be said that each of us is always perfectly certain as to what is happening in his own mind—in sleep and dreams, for example, *i.e.*, in the sub-conscious? Whoever answers in the affirmative is deceiving himself.

There is one fairly sharp distinction between all animals and any man except the most primitive, and that is written or hieroglyphical tradition; but it gives us a false impression of our own value. The spoken word flies away but the written word remains—so even the ancients declared. Indeed, our much-vaunted civilization lives and progresses only upon the fruit of the mental efforts of countless ancestors, accumulated in books. This it is which some describe euphemistically as human *perfectibility;* but it has nothing in common with heredity. The discovery of printing has meant a gigantic stride along the road of our perfectibility. The mental value of our brains may lag, by heredity,

behind that of the Chinese, the Persians and the ancient Greeks, even while our perfectibility continues to advance. Let us take heed! Decadence is knocking at our door, if she has not already entered fully into the energies of our hereditary mneme, where she will make her reverberations felt at a later date in the acquired material of our ontogeny.

II The Rôle of Ants in Nature

In the second edition of his admirable book *Des sociétés animales* (Paris, 1878), Alfred Espinas quotes various observations from my *Fourmis de la Suisse* (1874) and then expresses himself as follows:

"The superiority of the ants rests on their terrestrial life. This assertion may seem paradoxical, but one should consider the exceptional advantages which a terrestrial medium offers to the development of the intellectual faculties, as compared with an aerial medium. The air means long journeys undisturbed by incident, vertiginous vagabondage, far from the domain of real objects, instability, roaming, perpetual forgetfulness of things and of oneself. On the earth, however, there is no movement that is not a contact and does not yield precise information; no expedition fails to leave some memory behind it; and as there are limits to the possibility of roving, it is inevitable that some features of the ground which is incessantly traversed should be graven, with all its resources and dangers, in the imagination of the animal. Thence comes a much closer and more direct communication with the external world. Moreover, it is much easier for the terrestrial animal to utilize matter than it is for the aerial animal. When it is necessary to build, the air-creature is obliged either to secrete the substance of its nest, like the bee, or to seek it afar off, as does the bee when she gathers wax, or the wasp when she gleans the

elements from which her paper is made. The terrestrial animal has the materials for its work near at hand, and as these materials are varied, its architecture may likewise be varied. Hence it is probable that ants owe their social and industrial superiority to their habitat. If any one ant was ever the first to twist her wings about until she was rid of them, so that she might work more easily on *terra-firma*, she rendered a deathless service to her race. But it is not likely that things came about in this way, in this case or in others.

Our first example of property is set us by the ants. The lower animals possess nothing but the soil they occupy. The ants, as they ceaselessly furrow vast stretches of ground with their convoys, appropriate it to themselves without occupying it permanently. This earth is theirs because they are fixed to it and have their dwelling in it. Property appears first, therefore, as a direct effect, and then as the extension of industry. The ground over which the workers circulate regularly in their long files bears, in some measure, the faint imprint of the organization which is stamped so clearly upon every part of the nest. This ground is an instrument for the use of ants, like the nest itself, though to a less extent. The beaten paths are, in fact, extensions of the galleries, and the ants are prepared to defend them, like the galleries themselves, from the invasions of strangers. Just as the different parts of the nest communicate with each other, so does an uninterrupted current of information unite the pathways and the formicary. Thus animal activity conquers the soil and incorporates it with its own organism.

Whereas wasps and bees of different species can carry out only a few activities, nearly always similar in character, ants apply their energy in an almost indefinitely variable fashion to all the circumstances which face them. Some of them dig, others sculpture, others build, others heap up material, and

many of them hunt; there are ants which gather and store seeds, and suck the juice from flowers, and ants which nibble their petals: sometimes we see them capturing slaves, at other times rearing aphids, and all these various actions are susceptible of unlimited modifications, according to inherited tendencies and special circumstances. As a result of this power to vary the effect of their activity, the division of labour must be carried to a much greater length in a formicary than in a hive. In fact, if we were to examine a working formicary, we should be able to distinguish several categories of workers. But this division of labour (and here we have a feature peculiar to highly-developed organisms) has nothing rigid about it and involves organic modifications in a comparatively restricted number of species. M. Forel shows in his criticism of Lacordaire that a very small proportion of native formicaries exemplify the morphological differentiation into four kinds of individuals: males, females, workers and soldiers. He has observed it only in *Pheidole*."

It is a fact that ♂ and ☿ ants exercise no dominion over the air in their nuptial flight. But Espinas forgets to mention water, especially the sea, which is dominated neither by ants nor by men, except for ships and submarines in which man bears cosmopolitan ants against his will. We must not exaggerate in anything. Ants, moreover, are not mistresses of the 'sub-soil' as Bergson claims in his *Evolution créatrice*, but only of the surface of the soil and of plants, and then not everywhere. In the sub-soil, it is rather worms, moles, field-mice and microbes which tend to rule. Nothing of it is owned by ants but their scattered nests and a few passages. Furthermore, we have proved that Iceland, Greenland and Kerguelen contain no ants. In cold countries in general, as well as in the Swiss Alps at a height of

2,000–3,000 metres, the sway exercised by the ants over the surface of the soil is very modest and limited. But as the temperature increases, this sway becomes more and more marked, even in our temperate countries. The Brazilians say that ants are the veritable queens of Brazil, for they have more power there than any other creatures (Heer). This statement, as regards the surface of the soil and of plants, as well as plant-cavities, is true for all tropical and sub-tropical countries.

As I said in 1874 in my *Fourmis de la Suisse*, in the domain over which they rule, the ants' most dangerous enemies are other ants, just as man's most dangerous enemies are other men. In the same work I also said: "Every formicary which is at all considerable has its domain, its territory, which it seems to regard as its property. This is a direct result of the fact that all formicaries (I would now add except in the case of parabiosis) are enemies to one another. Thus a large *F. pratensis* colony may possess a whole meadow, several trees, or a hedge; and from this domain all colonies of other *pratensis*, *rufa*, *sanguinea*, *truncicola*, *Dendrolasius fuliginosus*, etc., will be excluded."

Ants, therefore, were the first landed proprietors, before man came into being, as Espinas strongly confirms. They were also the first collective shop-keepers. This was proved to us in Chapter II, where we saw how *Messor* colonies steal one another's stocks of grain.

The might of the ants derives from a vast number of facts enumerated in our work, particularly in Chapters I and III of the present volume. Here is one more example. "I myself once saw some *Formica pratensis*, which had lengthened one of their roads on account of the growth of their colony, come in contact with a nest of wasps (*Vespa germanica*) built in the earth, block up the opening and finally drive away the

numerous inhabitants, not without the loss of many combatants" (*Fourmis de la Suisse*, Part IV, Chapter II).

In his *Ants*, Wheeler remarks that their predominance is clearly indicated by the small number of their enemies (apart from other ants): a few special mammals, a few birds and reptiles and few insect parasites. To these we may add a few other insects, such as the Ant-lions and Hister. The integuments, bodies and habits of a host of animals are characterized by a whole scale of adaptations for defence and protection against ants, and this confirms the hegemony of our little friends within the above-mentioned limits.

This scale, as Wheeler says, also confirms the importance of ants in natural economy.

Ants, however, have no sway upon the earth over microbes or large animals. But they are our rivals in various respects: the *Messor* steal 'our' seeds, which they regard as 'their' seeds, in defiance of the Talmud; the *Attini* cut leaves from 'our' trees and 'our' vegetables, which they likewise regard as 'theirs'; and the European *Lasius* imperil our crops by covering them with their aphids and coccids.

The hunting expeditions of the *Dorylinæ*, described in our first chapter, as well as those of the *Ponerinæ*, would seem to prove that primitive forms, in ants as in man (as Wheeler remarks) lived by rapine and were carnivorous. These were gradually supplanted to a greater and greater extent by the omnivorous harvesting or farming animal-forms like the *Myrmicinæ*, *Dolichoderinæ* and *Formicinæ*, which, as we have seen, are the most recent ants. The analogy with the development of our human civilization never fails to be very striking, but with the ants progress is attained through heredity and not through acquired perfectibility.

If we regard the matter from the sole and very narrow point of view of our purely human social utilitarianism, the

question presents itself in the following somewhat different guise: 'Are ants *useful* to man or are they *harmful?*' The question is very complex. The answer to it varies according to the ant-species; and furthermore, when we attempt to destroy or conversely to propagate any special kind of ant, we are confronted with insuperable difficulties resulting from the tangle of the phylogenetic adaptations produced millions of years ago in the habits of various living creatures, animal and vegetable. By trying to disturb their natural hereditary equilibrium, we incur a danger of increasing the evil we wish to combat; and while we are endeavouring to afford artificial protection to animal or plant races chosen entirely with a view to our human advantage, we forget that we have weakened them and rendered them incapable of fighting alone against their natural enemies.

Bos, as we saw, proved that a field of beans protected from ants produced an infinitely better crop than one in which the *Lasius* cultivated their aphids. Here we have an undoubted fact. But by thus protecting the beans from the aphids, in the course of generations we weaken their power of resisting those enemies.

On the other hand, Ratzeburg was right when he published laws in Prussia forbidding the systematic destruction of the nests of the useful *Formica rufa* by bird-fanciers. As a matter of fact, *Formica rufa* is the *natural* protector which saves the forests from destruction by the *Bostrichus* (beetles). In this case it was the bird-catchers who disturbed the natural equilibrium, and Ratzeburg merely re-established it. I will limit myself to these two examples, which reveal the fundamental aspects of the matter.

According to Magowan, a certain Chinese writer declares that in the provinces of Canton no cereal and orange crops are successful unless resort is had to the hill people, who

scour the neighbourhood for the nests of yellow and red ants, which are then brought down to the plains and deposited on the orangeries. The ants thereupon devour the larvæ which ruin cultivated plants.

It may be stated as a general fact that in Switzerland, *Lasius* and *Tetramorium* are harmful to us and the *Formica* of the *rufa* and *exsecta* groups useful. The others are, generally speaking, indifferent. But, I repeat, this purely utilitarian human point of view must not be confused with the rôle of ants in the general natural economy of the creatures living in our world, especially in the tropics.

III Ants, Termites and Man

Every social cosmos is in itself superior to every individual cosmos, as much on account of the elasticity or separate mobility of its parts as of the specialized function of each. We have seen how an association of cells formed a coherent whole, with organs admirably adapted to their functions. But in this case, all the individual cells are imprisoned in their organ, and together they constitute a socialized individual, superior, certainly, to the cell, but inferior to a mobile association of its peers. They have become incapable of combining to form an immobile whole. Such mobility is a force, but in it lurks a danger.

The advantage of higher societies is made evident to us in the grouping of higher animals—the herds of bison or buffaloes, for instance, or those formed by elephants, making them the rulers of their forests; in the flocks of birds, still more in termites, and most of all in ants, the queens of the virgin Brazilian forest; evident, too, in civilized man, who aims at ruling the whole earth. In a word, 'union is strength.' Even lions and tigers which live in isolation dominate nothing but a few victims, isolated like themselves. The

same obtains with the gorilla, and with primitive man in his cave.

The organization of cells united in a single animal body was gradually formed by pure heredity in the course of millions of years. Hence it is due to the *slow combination* of engrams acquired in the individual mneme of each generation with the engrams imperceptibly *accumulated* by means of germ cells in subsequent generations. These constitute the *hereditary mneme*, and gradually come into existence through *mutations*, as de Vries showed. Moreover, *natural selection* and the *struggle for existence* constantly conserve the mutations which are helpful to the species and destroy those which are injurious.

Does this also happen with *societies* of mobile individuals which are separated from one another? Does the superior being, advantageous to the species, progress naturally of its own accord, and does the undesirable being, injurious to the species, destroy itself of its own accord?

The answer is *yes*, or almost so, as regards ants and termites, in which, as we have proved, specific hereditary instinct directly actuated by sensory impression is a predominating factor. In these insects, the mobility of the individual has very little power to restrain an innate social discipline, adapted in an identical fashion to the body-form of each, as well as to its habits; hence their apparent individual intelligence is almost exclusively fixed and adapted by heredity; very little room is left for the truly individual memory and variability of judgment in cases of doubt and the unforeseen.

For man, the answer is *no*—why, we shall shortly explain.

ANTS AND TERMITES. In tropical and sub-tropical countries, the sway of the ants over the little world living on the surface of the earth and of plants is *unlimited*, whereas

that of the termites is *limited* to the mound and passages of every termitarium built underground or in a tree. It is chiefly on account of their cruel enemies the ants that the termites are obliged to hide in this way. For further particulars I will refer the reader to Part IV, Chapter IV, as well as to the Appendix at the end of this volume, by Prof. Bugnion, entitled "The War between the Ants and the Termites."

ANTS AND MAN. Among ants we find weavers, butchers, cattle-rearers, masons, road-makers, harvesters, bakers, mushroom-farmers, excellent nurses of various kinds, gardeners, warriors, pacifists, slave-makers, thieves, brigands and parasites, but we find no professors, orators, governors, bureaucrats or generals, nor even corporals, nor do we find capitalists, speculators or mere swindlers. Think carefully about that, dear reader, and it will give you the key to the mystery.

The resemblance between a society of ants and a society of men is no mere matter of appearances, any more than the difference between them. Both depend on profound causes, hereditary or acquired, which we have now to analyse seriously; we have already done so to a certain extent, and it remains for us to show in detail how, in the phylogeny of multicellular living creatures, to use the words of Wheeler, there is "a shifting of proclivities from the *egocentric* to the *sociocentric* plane." The great variability of their instincts, the generally omnivorous capacities of their digestion, the multiplicity of their species (nearly 4,500, not counting races or varieties), their longevity, the relative stability of their colonies and their distribution over practically the whole world give the ants a great *social force* which other social insects possess in part only.

According to Wheeler, both ants and mammals seem to have appeared during the period which we call mesozoic or

secondary, when life first began to blossom throughout the world in its full glory. As the same author shows, the formicary is a society of females and their polymorphous derivative forms, in which the stupid male plays but an accessory part as a humble follower. The two human sexes, on the other hand, are complementary to each other, their mental faculties being, generally speaking, equivalent. The hereditary social instinct of ants permits them to live without chieftains, guides, police or laws, in an admirably co-ordinated state of anarchy; human beings are absolutely incapable of doing this, and if they attempt as much they at once fall back into such a triumphant state of brigandage that they are compelled to submit once more to the rule of chieftains. Such is the ancient tragedy of humanity, a thousand times repeated throughout history.

In my treatise on the Mind and the Brain (*Gehirn und Seele*, originally read in German in 1894 before the Naturalists' Congress at Vienna) I made the following remarks:

"The study of evolutionary phylogeny in animal biology leads us to feel sure that the *primordial* activity of the neurocyme (electrons of the neurones) is plastic (not reflex). But its elements were so few and the exigences of its environment so many that it was obliged to form specialized hereditary automatisms (instincts). *However, the difference between these two kinds of nervous activity is only relative.* We can observe such transitions in ourselves in all their initial stages, whether they be centrifugal or centripetal (technical routine), or central (abstract reason)."

At the present time I can only say that I entirely confirm this statement, printed twenty-eight years ago.

Rivalry and warfare between different formicaries can never cease, for these reasons: (1) Their instincts, like

their reactions to strange odours, are too precisely fixed by heredity (Part IV, Chapter II); (2) the number and diversity of their species is much too great; (3) even if their mentality were capable of such a thing, they are much too small to set up an international alliance among themselves throughout the world, in the manner indicated in Part IV, Chapters I and II; (4) above all, the mentality acquired by their small brains is absolutely incapable of comprehending what might really be the world-cosmos and internationalism. We have only to mention such a ridiculous idea to make every one laugh at its absurdity. Do not forget that it is scarcely 400 years since we human beings were enlightened as to these two ideas by Columbus, Galileo and others.

A written *tradition*, even an antennal tradition corresponding to our oral tradition, is excluded in the case of all ants. And in spite of this fact, the social cosmos of a formicary is very much superior to our states, societies and federations, from the point of view of order, organization, and the social work of the united entity. Why so?

Well, dear reader, it is because man's hereditary nature, deep-rooted in his brain, makes him an egoistic, individualistic, fierce, domineering, tyrannical, jealous, passionate and revengeful being, who wishes to enjoy liberty by the abuse of his neighbour's toil. For the slightest social defects possessed by this neighbour he is argus-eyed, but he unconsciously misinterprets or extenuates his own faults. For his personal satisfaction alone he chooses a few friends or companions and one or several sexual help-meets. It is comparatively rare for even his family to be united. Yet there are some men, and more especially some women—though they are exceptional—it is true, who devote themselves to the social well-being of humanity and are perpetually denying themselves for the sake of their

neighbours; but the masses misunderstand and persecute them. Moreover, when they attain 'power' success intoxicates them and turns their heads; rare indeed are those who resist, keep their integrity and persevere to the end along the path of true social service. What must we do, then, to grow nearer to the ants and yet remain men? Such tragic events as have lately befallen us in the so-called world-war of 1914 and the social war which has followed it since 1919, are of a nature to set us thinking and pondering over the human social question. And with this matter, in so far as light is shed upon it by our little friends, I should like to end my book.

HISTORY OF HUMAN PERFECTIBILITY. Here in the first place we must admit that we know absolutely nothing about the history of actual primitive men, such as the Neanderthal man or him of le Moustier. We can only assume that they possessed a mentality similar to that still found in the lowest living races, such as the Australian natives, the Veddahs of Ceylon and the dwarfish Akkas of the Congo, because the cranial capacity of these two kinds of human being proves a very small brain, comparatively speaking. Races of this kind which still exist are fast dying out, and vary enormously. The Akkas, one of whom I myself saw at the Congo Exhibition at Tervuren, are always in motion, and the first thing one notices about them is their changeable temper, which is choleric, aggressive and warlike. The Veddahs, on the contrary, are nonchalant and mostly apathetic, like the Chimila Indians recently extinct in Colombia. But both are intellectually inferior, the Veddahs, for instance, being unable to count beyond twenty. The Australians, for their part, have much in common with the fossil skulls of Neanderthal man. The cranial capacity of these still living primitive men is on an average 230–250 c.c. less than our own; and

the weight of their brain is 230–250 grammes; the Neanderthal skull is only about 300 c.c. less than our own (1,230 instead of 1,530). From the standpoint of theory, Emery, in his "Les Insectes sociaux et la société humaine" (*Revue d'Economie politique*, Paris, 1901, p. 15), has described the origins of human perfectibility under the rubric 'the instinct of progress.' The phrase is rather original.

Dubois' famous Pithecanthropus fossil, discovered at Java, with its cranial capacity of 850 c.c., constitutes a real transition between the higher apes (orang-outang, gorilla, etc.) and the primitive Neanderthal man. Can the 'instinct for progress' have originated in this creature? I would beg my readers to note that according to the data supplied by competent anthropologists (Klaatsch, for instance) the Pithecanthropus lived more than one and a half million years ago, whereas the man of the Neanderthal caves, of Le Moustier, Spy, Aurignac, Cro-Magnon, Grimaldi, etc., some of whom were found in the company of mammoths, lived more than 500,000 years ago. And even at that date, they left with their remains certain artistic ornamental figures, representing admirably, among other things, mammoths (which are now fossils), horses, horned men, etc. Hence even then there was some glimmering of the civilization whose development is now incalculable. In fact everything visible and sensible which man, however primitive, was able to *leave* to succeeding generations, could be *imitated*, *repeated* and *perfected* by these newcomers. Herein lies the beginning of the distinction between us and the higher apes, and herein the first signs of our perfectibility.

To this we must add that all the human races now living can combine to produce fertile offspring; it is impossible to

distinguish clearly the infinitely mixed strains in their descent; we are all 'half-breeds' and we are becoming more and more so, owing to the increasing facility of world-communication produced by our greater technical skill. But the farther back down the centuries we look, the more distinct and disconnected has been the localization of our races and varieties, a fact which explains how inferior races, whose phylogeny must extend for 500,000 years and more, have escaped destruction. The *cousinship* between the negroes and ourselves, for instance, must certainly reach back half a million years.

For the same reason, it is impossible to determine how direct or indirect is our relationship with our fossil ancestors of the Neanderthal caves, Spy, etc. But we must assume that if they were still living, we could combine with them to produce offspring, which we most probably could not do with gorillas and orang-outangs, or even with the pithecanthropus if he could come to life again in our own time.

The hieroglyphics and artistic remains of fossil men are all that enable us to judge whether their civilization was equal, inferior, or superior to that of any particular present-day race. Certain carvings by fossil men dating back half a million years are beyond the capacity of a Veddah or Akka, if not a negro. Hence the date at which human perfectibility began is obscured by the darkness of time, and varies from half a million to about a million years.

It is not until long after the first period, known as the Stone Age or diluvian Paleolithic Age, that a forward movement in civilization, or in other words perfectibility, can be more or less proven in the case of certain human races still very imperfectly distinguished from one another. In the later age of polished stone, we can also trace the appearance of ceramic art, which proclaims a notable

advance in civilization. Competent experts date this age between 25,000 and 15,000 years B.C. After that came various periods known as the Copper Age (3,000 B.C.), the Bronze Age (2,500 B.C.) and Iron Age (1,000 B.C.) characterized by the use of these metals by men for their various instruments of war or agriculture, as well as for ornament. The remains of these instruments and the sculptured hieroglyphics, which students are learning to decipher, have made it possible to follow step by step, after the late Stone Age, the still slow but gradually accelerating steps in the progress of our cultural perfectibility. Thus the age we call prehistoric is gradually transformed into the age we call historic, at first by means of hieroglyphics and afterwards by means of a few manuscripts preserved on papyrus. Modern Chinese and Japanese script is still very symbolic, and slightly reminiscent of certain hieroglyphics. The oldest civilization, nowadays quite historical and more or less surely deciphered, is that of the Egyptians. It reaches back to King Menes, 3,900 years B.C.—that is, more than 5,800 years ago. The history of Babylon is not so old, nor that of Assyria, and the record of the Chinese dynasties scarcely goes back to 1,800 B.C.

It can be proven in nearly every case that the nomadic life or that of the hunter preceded the sedentary and agricultural life, and that the matriarchal stage preceded the patriarchal. But as we behold the slow and tortuous ascent of human perfectibility from its infancy upwards, and of those lasting products which it bequeathed to its progeny during the periods which we regard as retrograde, and which may be called 'medieval' or 'barbarian,' we also behold in our ancestors, the offspring of primitive man, an abominable ferocity which makes the orang-outangs, chimpanzees and even gorillas seem perfect angels in comparison. When

primitive man came down from the tree-tops some millions of years ago, he entered into conflict with the monstrous mammals of the Tertiary Period, a time when force was the only law. At what stage the clan and the tribe succeeded the primitive family, we are quite unable to determine. But one thing is certain: the path of change was no peaceful bed of roses.

Thus the primitive male learned to wage war upon other living creatures, including his fellow-men, whom he would make into slaves when victorious or eat along with the rest. Courage, strength, skill and cunning were his prerogative. As woman was weaker than himself, in many lands he acquired the trick of depriving her, little by little, of her primitive savage rights. He made her his slave, entirely devoted to work and the sexual pleasure of her lord and master the male. There is no form of sexual aberration, even the most refined in character, which was not invented by the barbarian, even in the most distant epoch. One has only to read Otto Stoll's 1,000-page work, *Das Geschlechtsleben in der Völkerpsychologie* (Sexual Life in Social Psychology) to be enlightened on this subject. Moreover, the natural man's passions of hatred, jealousy and spite led him to invent the most atrocious forms of torture to wreak his vengeance upon his fellows—even the use of ants, as we saw in Part V, Chapter I. The fossil human remains which are taken from caves and ancient tombs are continually mixed up with weapons and mutilated skeletons. Furthermore, the history of the American Indians, Africans, etc., is crammed just as full of horrors as those of the Asiatic and European races. We are all about equal in this respect—and the war of 1914 gave us a new proof of the fact.

It is clear, therefore, that the sentiment of patriotism was at first only an extension to a few men of the primordial

family sentiment, and that it originated in the clan, where heroism and patriotic devotion dawned side by side with cruelty and vengeance. Hence militarism, the source of all cruelty, was inseparable, at any rate to begin with, from patriotism.

Not until much later did sedentary and agricultural life attach these sentiments to the soil, the hut, the territory of the clan, which had become the tribe, and eventually the kingdom. In its early stages, the social instinct of the human family was so rudimentary and so entirely the slave of force, that it could not exist without a single male chieftain to rule the group. And following his hereditary nature, deep-rooted in his mneme, this chieftain always oppressed his subordinates, his women-folk and his children to a greater or less extent. This was the origin of polygamy, which, like the kingdom, was based on the patriarchal system. If the patriarch, tribal chief or king was weak or idle, he became degenerate and was overthrown, just as the 'rois fainéants' were afterwards overthrown in France by the 'maires du palais.' This accounts for the fact that the republican form of government was slow to appear on the human stage, and was at first only the exceptional product of an advanced social organization, with a tendency to grow disorganized and fall back into monarchy owing to the corruption of the officials elected to govern it. The whole history of human races proves to satiety that we are absolutely incapable of living in the happy and well-co-ordinated anarchy represented by a formicary, and shows how misguided was the all-too-famous Kropotkine. The increasingly rapid development of our perfectible civilization has led us to an *impasse*, since our fierce, individualistic hereditary nature has been unable to keep pace with the rapid enlargement of social requirements, and takes a hundred thousand years in which

to be sensibly modified by acquired engrams. Man is born good, said Rousseau, but he is corrupted by society! This is one of those supreme absurdities which have been canonized by the countless repetitions of unthinking people, and it is high time that we corrected it.

IV What Can We Hope for the Future of Humanity?

How are we to extricate ourselves from the tragic dilemma whose causes we have just outlined?

Setting aside the inferior races, whether living or fossilized, let us devote a few words to the known history of our civilized nations. Here we find human pride creating out of its own imagination the sectarian dogmas, wrongly termed religious, devising out of the fear of unknown forces an all-powerful 'God' in man's own personal image, and at the same time generally explaining away all his social ignominy by attributing it to another imaginary being called the 'Devil.' In reality, owing to our lack of social instinct, a personal God and Devil subsist on more or less friendly terms in every human brain, and the *Universe*, that power which we find so unfathomable, belongs to an unknowable metaphysic. What we need is a true inter-sectarian religion of social human welfare. This religion, being built on the love of our neighbour, must be exempt from sectarian strife between the *dogmas* wrongly described as *religious;* we shall return to this again. Mohammedanism and its harems provide us with example of the oppression of woman.

The large empires, ancient and modern, whether or not they consist of a federation of kingdoms—and especially China—provide striking examples of progressive degeneration due to the abuses of their autocratic government. In spite of the lofty view-point of Confucius and Buddha, the Chinese, surrounded by their wall and separated from

other nations, oppressed by the Manchu dynasty, swarming with superfluous population, gradually fell, despite their toil, into a state of stagnation which became degeneracy. For all their intelligence, perseverance and great brain-power, they became congealed within their narrow confines, and their civilization, like their religious forms, moved backward. For varying causes, the empires of the Assyrians, the Pharaohs, Alexander, the Romans and the Persians deteriorated and were destroyed. To-day those of the Turks, the Hapsburgs and the Czars have disappeared, while the German Empire has become a republic like that of Napoleon. We find republics, too, suffering from social maladies similar to those of kingdoms and empires. Nevertheless, Switzerland and the United States have proved one thing: States or cantons in union may enjoy a fairly lasting peace *among themselves*, provided they are subordinated to a superior force, and, furthermore, endowed with certain fundamental liberties in connection with rights, languages and beliefs, accorded to all their individuals, who are thereby constituted citizens.

By *eugenics* (*Galton*) we mean the slow *hereditary* amelioration of our human races, in all physical and mental respects, by means of a wise artificial selection; that is, by wise intermarriage and a wise choice of individuals to propagate their kind. To all action which has the effect of a prerogative upon our heredity, on the other hand, I have given the name of *cacogenics*. Warfare between primitive men improved their strength, skill, guile and intelligence, and the size of their brains by eliminating the weakest and most stupid among them. But it debased and ruined their social sense and their willingness to work for a good end, so that its action was eugenic on the one hand and cacogenic on the other. Modern warfare, however, conducted by a general with

cannon and shot, picks out for sacrifice the men who are best in every way, and is entirely and immediately cacogenic. This was proved by the world-war of 1914, better than ever before.

Here we come to the most distressing questions that face present-day humanity as a whole. Our civilization and our intellectual and technical perfectibility are apparently still increasing, even with gigantic strides, owing to printing, libraries, electricity and devices for transport. But instead of increasing in itself, the overworked brain of present-day man is becoming enfeebled and, on the whole, deteriorating in hereditary value; it is probably less on an average than that of our ancestors in the time of Confucius, Socrates and Marcus Aurelius. It simply cuts a spectacular figure by reason of the treasures bequeathed to it by its ancestors, whom it can do little more than plagiarize. This is certainly a hard word, but I think it is true.

An international society of nations is being constituted at the present moment. It has become inevitable; but our problem is, how to give it an organization which will prevent it at the very start from going the way of China, becoming degenerate and corrupt, and thus covering the whole human race with the shadow of its misery and disaster.

At the end of his *History of Materialism*, Lange wrote:

"We lay aside the pen of criticism at a moment when the social question is stirring all Europe, a question on whose wide domain all the revolutionary elements of science, of religion and of politics seem to have found the battlefield for a great and decisive contest. Whether this battle remains a bloodless conflict of minds, or whether, like an earthquake, it throws down the ruins of a past epoch with thunder into the dust, and buries millions beneath the wreck, certain it is that the new epoch will not conquer unless it be under the banner

of a great idea, which sweeps away egoism and sets human perfection in human fellowship as a new aim in the place of restless toil, which looks only to the personal gain. It would indeed mitigate the impending conflict if insight into the nature of human development and historical processes were more generally to take possession of the leading minds."

We must needs accept the challenge, seeing that Lange's prophecy, written in 1874, came to pass between 1914 and 1923, in the sea of blood poured out by twenty million slaughtered human beings. One question takes precedence of all others: In the future society of the nations, what must be centralized and what decentralized?

The first work of centralization should be brought to bear upon a great supernational army, which is absolutely necessary to subdue the present absolute rule of the fierce national groups of human wild beasts known as States. This supernational army, commanded by a pacifist general and admiral, must always be ready and capable, until the enormous majority of States have gradually rallied to it. Then, and then only, it will require some fifty to a hundred years for such an army to be relegated to a museum of antiquities, for its only use thereafter will be to fire guns at the moon or some planet. Furthermore, supernational laws must establish various individual liberties, in such a way that no state will have any more power to suppress or disturb them; this will be the great task of a world-council. These liberties are: (1) civil liberty for men and women; (2) liberty of language; (3) liberty of belief; (4)proportional representation of minorities; (5) the right of groups calling themselves national to separate themselves from a State by the plebiscite; (6) the right of the people to socialize private property in some way or other by vote of the majority of individuals, etc.

On the other hand we must decentralize the Universities

and scholastic authorities of all ranks, in order to free them from every bureaucratic yoke and from the terror of examinations, at the same time organizing them on the model of the 'New Schools' with a minimum of obligatory instruction. We must in a general way disestablish all the autocracies and bureaucracies of States, provinces and even towns, and give normal individuals of both sexes a corresponding increase in freedom and responsibility, from youth upwards. We must disestablish all obligatory creeds and substitute freedom of individual belief assured by law. We must not imitate the centralization of French intellectualism in Paris; it has done a great deal of harm to France and to independent thinking even in Paris.

Thus in a word the supernational authority, directly elected by the nations, will in no sense of the word oppress them and must be merely a federation so organized as to safeguard liberties and their truly national aspirations against the arbitrary tyranny of States. It is for this purpose alone that the sovereignty of States should be limited, which means that it must be an improved form of that of the Swiss cantons and of the United States of America; the present States must continue to exercise only relative sovereignty.

In spite of all his bad antisocial instincts, man can be tamed, owing to the individual plasticity of his brain, but only by means of a good social organization set in action by various means to which I have alluded above, and others also. It will be chiefly at a later date, after the definite cessation of wars between States, whose limited supremacy will be placed under the ægis of a world-council freely elected by all nations, and the protector of their liberties, that humanity will find itself able to make real progress. But any such supernational organization must be sustained. For this purpose every State must be required to enforce a

minimum of *obligatory work* upon all healthy individuals, whatever the nature of the social service.

One human formicary, united throughout the whole world, and at the same time divided into a host of multicellular individuals, townships, nationalities and States superimposed upon one another, but supple in their restricted liberties, will replace the barbaric conditions of our ancestors and all their warlike anarchies. It will free humanity from a great deal of distress, without, however, realizing the Utopian ideals of certain visionaries for a quickly-approaching earthly paradise in which all men suddenly become angels. No—we shall always have need, alas, of laws, tribunals and police, even prisons and madhouses, by reason of the pitiless heredity of our innate feelings. But all these things must be completely reformed. Many lunatic asylums have already set us good examples in this respect. We may hope that the eugenics of the future, if well applied, will even be able to improve by small degrees the quality of our higher races. Such a social cosmos in a supernational human formicary, united by federation throughout the world, is a real possibility. It is even certain to come to pass, however painful be the process of its gestation by a scarce-conscious plurality of rulers, whereas our little friends the ants are, most fortunately for us, incapable of it, and we have seen why.

International Parabiosis of the Nations of the World

Grotius in the 17th century, Béranger in the 19th and I myself in 1914 (in my 'United States of the World,' *Etats Unis de la Terre*) dreamed of such a Utopia. But, long before any of us the ants had realized the true universal fraternity in equality and liberty, in the form of *parabiosis* for communal work. Work in the midst of general peace is the true

liberty. But in man, unfortunately, this social work must be obligatory. The reign of idleness and its privileges must cease, for at all times and in all places they lead to degeneracy in the individual, as with the 'rois fainéants,' or in the race, as with *Strongylognathus testaceus* and finally *Anergates* (see Vol. III, Chapter VI).

Nevertheless, as a basis for education, this kind of obligation, if well co-ordinated from childhood onwards with the hereditary aptitudes of each human being, ceases to be the drudgery nowadays described by our reactionary and retrograde capitalists in the hope of terrifying the people. Rather does it become a secondary automatism, so beneficial that the individual can scarcely dispense with it in later years.

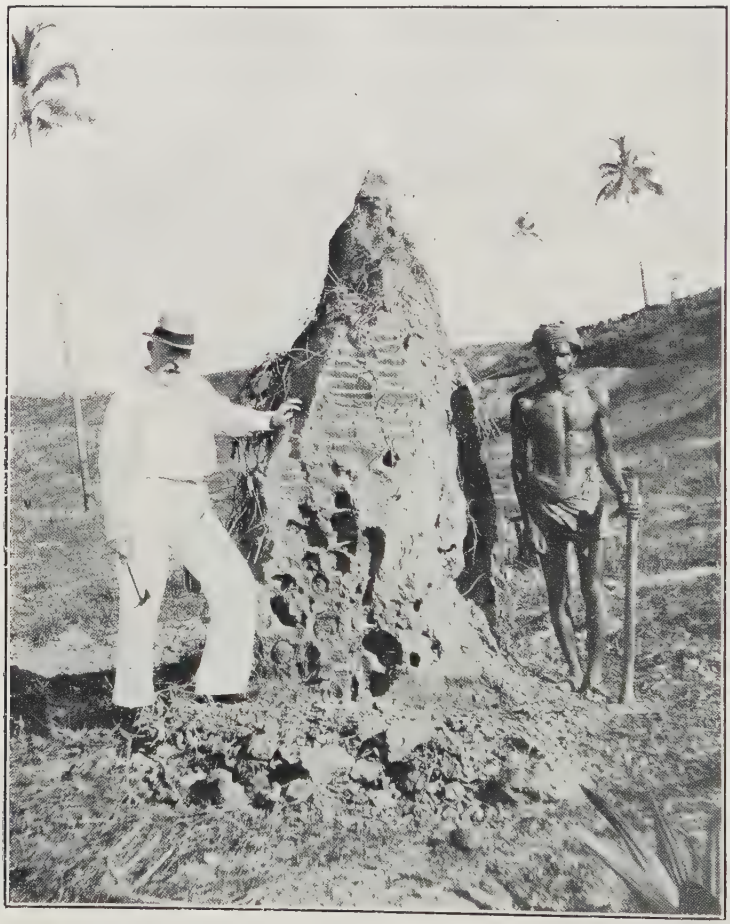
I myself have found that certain elderly workers who have amassed great wealth in the illusion that they would find happiness in the evening of their lives, become the victims of the most fearful neurasthenia, caused solely by the inaction which they had at last attained after desiring it so long.

Given the passions and weaknesses of man, however, we must fight with all our strength, by means of good legislation, against all the social causes which enflame our unwholesome passions—such as alcohol, narcotics, gambling, debauchery and luxury, for these are the worst hindrances to the social well-being of all in that peaceful federation of nations to which we must aspire. *The scientific religion of man's social well-being*—this must be the religion of the future, and, like that of the Bahaïs, it must be free from doctrine and from metaphysics, uniting all that is truly good and purely human in the ancient religions. As for a God incomprehensible to man, whom some believe they can know or feel, whom many adore and others fear or even curse, and whom many people

bedeck with their human attributes—we may leave everyone free to adorn this idea with whatever metaphysics he pleases. The religion of the social well-being of man has no concern with Him: neither have I seen His temple among the ants.

Farewell, dear reader; I now lay down my pen. Ponder all this and grow wise, a true Linnæan *Homo sapiens*—that is, unless you are one already!

A. Forel



Nest of *Termes Redemanni* at Ambalangoda (Ceylon), after a photograph by C. Ferrière.

[*Dr. Bugnion is seen standing on the left of the picture.*]

THE WAR BETWEEN THE ANTS AND THE TERMITES

A STUDY OF THE ORIGIN OF INSTINCT

By Professor Edouard Bugnion

The Termites

Termites in tropical countries have no enemies more dreadful and more dreaded than ants. Between these two little creatures there is perpetual strife, an interminable war which has been relentlessly pursued for thousands of years. It is also a well-established fact that the highly ingenious and varied measures of defence devised by the termites are practically all intended to protect them from the attacks of the ants, their hereditary enemies.

Termites are social insects, and are always grouped in *colonies*. Every *nest* or termitary regularly contains three categories of individuals known as castes: the *sexual forms*, *workers*, and *soldiers*.[1] (See Plate XVIII.)

The sexual forms (male and female) have one function only, the reproduction of the species and its dissemination over a wider area. Derived from larvæ similar to those of the workers (their mouth-parts are identical), they differ from them inasmuch as they do not attain their permanent condition after a simple larval phase; but pass through a second stage, in the course of which the rudiments of wings, eyes, ocelli and sexual glands appear. The larvæ

[1]Although the workers and soldiers are usually sterile it has been observed that so-called asexual individuals, especially among primitive termites, are sometimes furnished with genital glands.

of the second stage, which are known as nymphs, and are recognizable by their wing-stumps, their long abdomens, their milk-white colouring, and their two small black eyes, undergo a supplementary moult, the chief purpose of which is to free the wings from their sheath. This moult, a slighter matter than the others, is only a change of skin, and takes very little time.

When they reach the state of perfect insects or imagines, the male and female sex-forms for the most part will swarm. It is at this stage that most of them escape from the termitary, rise up into the air in large masses and sometimes, attracted by the lamplight, invade bungalows.

The worker, an apterous, whitish creature, usually blind and without reproductive organs, may be regarded as a termite which has remained in the larval stage (arrested half-way). It is endowed with dentate mandibles for carving wood, and its principal mission is to gather wood-*débris* outside the nest, fill its intestine with it, and use the ligneous paste thus produced for constructing fungus gardens. It is upon the worker too, that the greater part of the work devolves; firstly, the labours of construction; secondly, feeding the queen and king; thirdly, 'licking' and transporting the eggs. The worker's life comprises two distinct periods, separated by a phase of immobility corresponding to a main moult. During the first period, the still soft and delicate larva, with its uniform white colour, is incapable of carving wood and lives on fungi. During the second, the termite, which has acquired horned mandibles and a more resistant head (yellow or brownish) is capable of carving wood and attending to the work which falls to its share.

The soldier is farther removed from the sexual form, and constitutes a separate type. Its head is hard and elongated,

Fig. 1. Winged sexual form × 3.

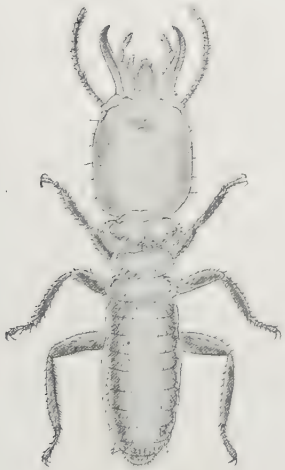


Fig. 2. Soldier × 6.

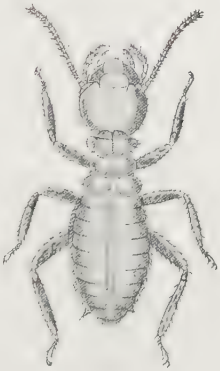


Fig. 3. Small worker × 8.

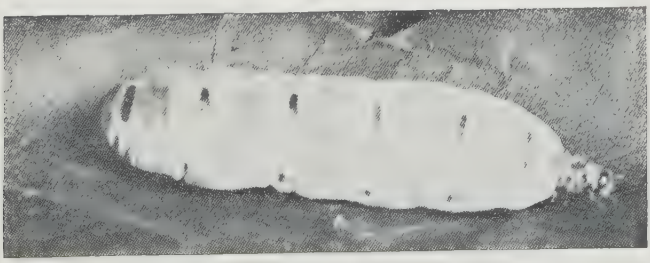


Fig. 4. Queen (natural size).

Termes Horni.

with a basilary plate[1] welded to the underside of the head. Its curved, sickle-shaped mandibles, ill-adapted for carving wood, are weapons of offence and defence. The soldier's task is to defend the colony (against ants, millipedes, etc.), and it fulfils this duty with a courage which is proof against all trials. It is more alert than the worker and has the moral guidance of the community as a whole. We shall presently see how the soldiers, in case of accident (destruction of part of the wall) bring the workers up to the breach and organize both the repairing and defensive measures. The soldier's life, like that of the worker, is divided into two periods, separated by a phase of immobility corresponding to the main moult.[2]

The following observations, mostly made in Ceylon in the course of four consecutive winters (1909-1913) are concerned with the defence-measures employed by termites in the wars which these insects have to wage against the ants.

1 We may take as our first example the *higher termites* or *dome-constructors*, represented in Ceylon by *Termes Redemanni* and *obscuriceps*. The dome (termite-mound) which is almost conical in shape and about 1-2 metres high, consists of fragments of earth stuck together with saliva, forming a hard mass which may be compared with cement. Its outer crust, 15-20 centimetres thick, is difficult to break down, even with a pickaxe. The higher termites are essentially fungus-growers. Their workers are constantly occupied in gnawing dead wood, and they use the half-digested pulp

[1]The basilary plate of a *Calotermes* soldier can be clearly seen in Figure 2 of Plate XXIV.

[2]The number of the moults is not yet exactly known, in the higher termites. According to Grassi and Imms, four to five moults have been counted in the case of *Calotermes*, and at least four in that of *Archotermopsis*, before their complete development.

(which contains spores) to form fungus-gardens, a sort of spongy mass (Fr. *meules*).

The termite-mound contains a large number of cavities or compartments intended for sheltering fungus, and these communicate with each other by very narrow passages. It is in the depth of the structure, at the level of the ground or a little below it, that the most numerous and largest compartments are found. There also we may see the most prosperous gardens. The number of compartments in a good-sized termite-mound may be estimated at over a hundred.

The gardens, an essential item in the termite-mound, are made of partially-digested wood-paste, emitted from the rectum of the workers in the form of brown dung, but treated again by the mouth-parts and stuck together with saliva. They are brown in colour, friable, and usually somewhat damp, have a multitude of cavities which add to the amount of surface available for planting and facilitate the access of air to the interior.

A garden that is being fully exploited—such as we find more especially in the neighbourhood of the royal cell—has both its external and internal surfaces covered with a delicate greyish mycelium, formed of interlaced filaments and bearing small white balls or 'kohlrabi heads,' about one mm. across, which I have called 'mycotêtes.' When these are viewed under a microscope, they display ramified stems laden with conidiophores and conidia (fungus-spores), which serve as food for the young and the royal couple.

The fungi found in termite-nests, according to J. Petch,[1] are of two different kinds, an agaric (*Volvaria eurhiza*) and a xylaria (*X.nigripes*). The agaric (when developed outside

[1] 'Insects and Fungi,' *Science Progress*, Oct., 1907.

an abandoned termite-mound) forms an edible cap-shaped fungus, brownish at the top, with white lamellæ, and reaching a height of 25 cm. Xylarias appear in the form of cylindrical, whitish stems, about as thick as a pencil, which become swollen and brown towards the tip.

Gardens placed under a cover for observation purposes seldom produce any agaric, but only xylarias. It is a curious fact that the white balls or 'heads' (*mycotêtes*: a special product of the agaric) do not flourish in laboratories, but soon undergo a kind of melting process. It seems as though the atmosphere of the termitary were indispensable to their success.

As for the sowing of the gardens, in my own opinion it goes on of its own accord, from the very first day, by reason of the conidia contained in the wood-pulp. When examined under a microscope, the contents of the worker's rectum certainly prove to include a large number of ill-digested conidia, apparently capable of germinating amid the wood-*débris*. Hence in order that the ligneous paste may contain a quantity of seed, it is only necessary for the worker termite to swallow from time to time, in addition to the wood-*débris*, a supplement of 'heads.'

Every termite-nest shelters at least one egg-laying queen confined in the 'royal apartment' in the company of her spouse. This worthy matron, in some species 6-7 cm. long, drags her enormous abdomen behind her, and is practically incapable of moving. If placed on a table, she can advance but a few steps at the utmost.

The king is smaller and more agile. He is sepia-brown, about 12 millimetres long, and resembles a perfect termite without wings, but with a somewhat larger abdomen than usual.

The apartment containing the royal couple is an elliptical

crevice, about 2 centimetres in height by 10-12 in width and depth. No spongy bodies are ever to be found within. Carved out of a hard, compact mass of earth, it lies at the bottom of the termite-mound almost on a level with the ground, sometimes a little above, sometimes a little below, the surface.

Its smooth, uniform walls are perforated with a large number of passages which allow the workers and soldiers to come and go, but are too narrow to enable the king to pass. He is shut up for life with his consort. The food of the royal couple consists mainly of *mycotêtes* (brought to them daily by the workers and soldiers) in addition, apparently, to a certain amount of saliva disgorged by these diligent caterers.

At times we find two queens instead of one enclosed in the same apartment with one or two kings. An apartment with three queens is a much rarer find, and an apartment with four queens is quite exceptional. Only once did I observe in the same cell (*T. Redemanni*), in the company of one king, four plump queens of practically the same size (4-5 centimetres).

The termite queen with her two enormous ovaries is, if I may so express it, a veritable egg-laying machine.

Escherich has estimated the number of eggs produced by the adult queen of *Termes bellicosus* at 30,000 a day. As the egg-laying process is continuous, this figure when multiplied by 365 gives 10,950,000 in one year, more than 150 millions to a single female, supposing that her life is prolonged for fifteen years.

When the naturalist approaches a termite-mound, he seldom sees a single termite outside. The dome certainly possesses a few fairly large passages (ventilation chimneys) opening on to the surface a little below the top and leading

to the depth of the interior. But these passages, which serve for the coming and going of the workers, during the period of construction, are always subsequently closed. If a few fissures are left for ventilation purposes, we may be sure that the soldiers guard them well and allow no intruder to enter.

The inhabitants of the nest (workers and soldiers) do not expose themselves in the open, but go to and fro through subterranean galleries on their visits to places near at hand, where they can cut pieces from dead trees and provide themselves with wood for the purpose of constructing their gardens. These galleries, which, so it is said, may extend for more than 100 metres, are completed by a covering of hard earth wherever they come near the surface. If, for example, a tree-trunk has been felled to the ground and lies ready to be exploited, large crusts of earth may be observed, filling the empty space (between the soil and the tree), and carefully blocking up the rifts in the bark, thus sheltering the workers from the ants.

The same dispositions are observed inside bungalows which are invaded by termites—by *Termes obscuriceps* in Ceylon, for example. The little cordons or tunnels of hard earth, which lead from the nearest nest to a chest placed on the ground or a picture hanging on the wall, and which betray the presence of termites, are manifestly protective measures. Their purpose is to enable the workers to exploit the contents of the chest or gnaw the picture frame, without being molested by red ants (*Œcophylla smaragdina*), the habitual guests of bungalows, which are much better armed, and would not fail to devour them if they were imprudent enough to move about in the open.

Very detailed precautions are likewise taken at the moment of swarming. Among others I may cite a few

observations made at Seenigoda on January 1st, 1912, during the swarming of *Termes Horni*, a fungus-growing termite, which does not construct domes, but is content with subterranean nests.

The termitary, which was entirely hidden, lay at the foot of the bungalow, partly under the turf and partly under the trench which served to drain off the rain-water. It was half-past six in the evening. Winged termites were seen coming out of two openings carved in the bottom of the wall, through the brick-joints. The holes were the size of a goose feather and just large enough for their passage. Each opening was surrounded by a yellow patch as large as a hand, formed chiefly of workers, with a relatively small squad of soldiers for the protection of the sexual forms in case of alarm. These creatures had to walk one behind the other, with their wings folded along their backs: but they moved so quickly that in half an hour's time several thousands had passed.

On reaching the open air, the termites beat their wings and fluttered at the foot of the wall for a few moments, then took to flight and soon disappeared above the house. In a short time, a number of swarms, attracted by the lamp-light, had invaded the verandah.

When I came back at about 8 o'clock, I saw that the exodus had ceased. I also observed that the two holes were blocked up with earth. In their terror of the ants which might have found a way in, the termites had taken the precaution of closing the holes when they withdrew. These defensive arrangements certainly seem to prove extraordinary sagacity.

The termites, with their soft bodies and unprotected abdomens, live in the midst of a hostile race. Fierce ants, ten times better armed and more agile, are lying in wait

for an opportunity of devouring them. And yet, except when a man's tool or an ant-eater's claw happens to make a breach in it, the nest, with its subterranean avenues and its vast system of cavities, is so well protected and guarded that its countless inhabitants develop and prosper within in the most perfect security.[1]

It is chiefly when some brutal interference suddenly deprives the termites of these protective measures that we are able to form a clear judgment as to their importance, and at the same time, of the ingenuity of the workers. An experiment which I made at Ambalangoda on December 25th, 1909, is particularly instructive in this respect.

The sky was overcast and the thermometer stood at 28°. The termite-mound (*T. Redemanni*) of yellowish earth formed a large cone a metre high, with several ventilation chimneys opening obliquely a little below the top. I cut into the wall with a hatchet and found, about 12 cm. down, a round chamber as large as an orange. The spongy mass inside this chamber remained intact. At that moment only a few termites could be seen on its surface. I removed the whole outer wall, swept away the *débris* and went away for a few moments.

On my return I was forced, somewhat against my will, to witness a real drama. Some very agile ants (*Plagiolepis longipes*), scenting good fortune, were already on the spot. Forcing their way into the chamber, which was now disclosed to view, they seized the young larvæ and stole away

[1]The only occasion on which termites (sexual forms) are massacred in very large numbers is during the process of swarming, when, having left the nest and suddenly found themselves deprived of all protection, they fall defenceless into the power of their sharp-toothed enemies. The facts are well known and I need not dwell on the matter here. We need only remember that nature, with her usual foresight, produces males and females in very large numbers.

as quickly as possible, carrying their prey. Had this daring raid been further prolonged it would have ended in a real disaster.

Though a little anxious at first, I was soon convinced that the industrious termites are by no means disposed to allow themselves to be massacred. As soon as they received warning,[1] a multitude of soldiers rushed up. Organizing the defence, they arranged themselves in a circle all round the opening, opened their mandibles and offered resistance to the ants.

The workers for their part lost not a moment in getting to work. They brought up little slabs of earth from the interior of the nest, moistened them with saliva, deposited them at the surface of the fungus-bed (which was still intact), and began to construct a system of pillars. In half an hour's time a sort of lace-pattern could be traced, formed out of damp earth, whose dark colour stood out clearly from the adjoining places. This lacework of earth was the first sign of an operculum or cover which was to be propped up in a few minutes on the pillars, leaving no sign of an opening.

A crack several millimetres broad, like a miniature trench, round the principal wall and the edges of the operculum, was occupied by the soldiers, which remained in circular formation all the time and opposed themselves unflinchingly to the invading ants. Remaining firmly at their posts, and protected by the trench in which they sheltered, they kept good watch until all danger was past.

Being pressed for time and somewhat stiff, I was not able to watch the repairing of the breach until the end.

[1]Under certain circumstances, the *Termes Redemanni* soldiers can emit a rustling noise, a kind of alarm signal, which the workers perceive by means of their chordotonal organs.

But when I came back a fortnight later, I saw that not only had the termites closed the chamber, but the excavation in the wall itself was also practically filled in. To achieve this last piece of work (the application of new layers to the outer surface of the operculum) they had, I believe, journeyed through small openings worked in the thickness of the new-formed crust or arranged on its periphery. It is indeed very improbable that the prudent termites ventured to the surface of their dome without reserving some means of returning thither as speedily as possible in case of alarm.

After satisfying himself (1) that the soldiers, whose duty it is to organize the defence, are absolutely blind and (2) that the workers whose duty it is to carry out the reconstruction are puny insects, 5 millimetres long at most, the biologist who witnesses an experiment of this sort is amazed and confounded. His admiration grows still further when he tries to discover the directing force which commands the termites and the moral bond of union between them—and can find nothing at all. At length he is forced to conclude that the actions of these little creatures (which seem at first sight to be co-ordinated and well considered) are, most probably, altogether instinctive.

2 Other examples are provided by *Eutermes*.

The genus *Eutermes* (Hagen's *nasutus*) is distinguished from other termites in that the soldier bears at the front of its forehead a projection (frontal horn) traversed by a duct. A contractile ampulla inside the head secretes a viscous fluid which flows through the excretory duct and exudes in drops at the tip of the horn directly the termite is attacked. As ants have a special dread of coming in contact with this liquid, it is a very valuable means of defence for *Eutermes*. For example, when an *Œcophylla* climbs along a trunk to attack *Eutermes monoceros* and

receives the contents of the ampulla full in the face, it falls almost immediately from the tree. Henceforth it is vanquished, and incapable of resisting. Whether it is the viscosity of the secretion which has this effect, or some special chemical action, the facts remain that if we follow the ant which has fallen on the ground, we see her busied for a long time in rubbing her mouth-pieces against stones, roots, etc., in the effort to free herself from the liquid which limes them.

Bathellier, the director of the Phytopathological Institute at Saigon in Indo-China, made a very convincing experiment on this subject. It was concerned with *Eutermes matangensis*, a wood-gnawing species which frequently installs itself in houses and causes serious damage. The following is an account of the experiment approximately in the author's own words :

"I took fifty *Eutermes* soldiers and enclosed them in a Petri dish in the company of six reddish, large-sized ants. After a few minutes I removed the cover of the basin and found my six ants all tangled up and scarcely able to move. One of them tried to stir, and a soldier immediately stopped her by thrusting its rostrum in her direction and giving her a douche. I observed, moreover, that there was no contact and that the rostrum of the *Eutermes* continued to point in front only for a very short time. Three of these ants were unable to leave the dish except with my assistance. Their mandibles were stuck together. Little grains of sand and minute fragments of wood stuck to their bodies, especially to their heads. Left unaided, the three others did not succeed in freeing themselves. The more they struggled, the more their limbs stuck to each other and adhered to their bodies. Soon they were rendered completely motionless, and finally they succumbed.

When observed under the microscope, the ants which had come in contact with the *Eutermes* soldiers proved to be covered with little round spots like drops of a very thick syrup. Owing to their viscosity, these spots, which were often confluent, had retained all sorts of *debris* which still stuck to the surface of the integument."[1]

As their cephalic ampulla provides them with sufficient armour, the soldiers of the genus *Eutermes* have, on the other hand, very reduced mandibles. When they engage in combat with ants, moreover, it is not with their teeth but with this ampulla that they strive to resist their aggressors.

The following observation upon some cocoa-tree termites (*Eutermes ceylonicus* Holm.) is very instructive in this respect.

This species, which belongs to the 'low country,' nests in the earth under the roots of the cocoa-tree, sometimes also at the foot of the Kitul palm, from which the natives draw syrup. The presence of these insects is betrayed by long, greyish cordons trailing along the trees and rising from the roots right up to the terminal bud. These cordons, which are almost as thick as a pencil, are so many little tunnels for the protection of termites (workers and soldiers), in the tree-tops, against the ants.

The *Eutermes* cordon, which is formed of wood-*débris* and grains of earth glued together, provides a precious source of study for the naturalist. It is only necessary to

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[1]This interesting observation vividly recalls the defence measures of the *Dolichoderinæ* (see Part I, Chapter IV, and Part IV, Chapter III) The secretion of the anal glands of these ants contains no acid; it ferments on contact with the air, and quickly becomes a resinous mass which impedes the antennæ of the enemy and puts it out of action, like the viscous fluid of *Eutermes* [Forel].

remove a small segment of the tunnel with a knife (preferably on the eye-level) and the work of reconstruction can be easily followed with the help of a lens.

An experiment of this kind was made on the plantation of Seenigoda, on December 19th, 1909, at 8 o'clock in the morning. It was a magnificent day. The thermometer stood at 25 degrees. The cordon facing the east was in the full glare of the sun. On scratching the wall for a distance of one centimetre, I first of all saw some dozen soldiers appear at the opening, then advance a few steps and arrange themselves in a circle, with their frontal horns thrust outside, ready to face an expected enemy. When I came back after a quarter of an hour the termites had all returned to the galleries and were already occupied in repairing the part destroyed. A row of soldiers remained at the level of the opening with heads thrust outwards and bodies withdrawn into the interior. They were waving their antennæ about vigorously while they chewed busily at the edges of the breach and moistened them with their saliva. A damp border, darker in colour than the rest of the wall, was already visible all round the hole. Soon there appeared a labourer of another kind, belonging this time to the worker caste. When she had recognized the place by means of her antennæ, she veered round sharply, turned her anal extremity to the breach, and deposited upon it an opaque drop of a yellowish-brown colour, expelled from her rectum. Soon after this another worker appeared, also from the interior, holding in her mouth a grain of sand, which served as a fragment of rubble and was laid on the droplet at the place assigned.

This performance was henceforth regularly repeated. For half an hour I was able to watch the alternation: first

one termite (worker) would inspect the breach, turn round and emit her yellow droplet, and then another laden with a grain of sand would place it at the edge. Some of them brought small scraps of wood instead of grains of sand. The soldiers, which were constantly waving their antennæ, seemed to be specially concerned to protect the workers and direct their work. As in the first place, they were drawn up in a line on a level with the opening, but they made way directly a worker came on the scene, and apparently directed her to the spot where her burden was to be laid.

I withdrew for a few moments on account of the fierce sun, and found on my return that the injured part had been almost repaired. A narrow slit, 2 or 3 millimetres long, was all that remained to fill up. Several pairs of antennæ still showed through this slit, but this was the only indication that the little labourers were moving about below. Still using my glass, I managed to see two or three yellow drops spreading out over the edges, and others trickling through the crevices here and there. A few grains brought from the interior were successively applied to the surface which had been smeared with glue, and that was all. The vault was now constructed, although it was somewhat more depressed than the rest of the tunnel. The repairing-work, which had been carried on entirely from within, had lasted an hour and a half; soldiers and workers (relatively few of the latter) had shared the labour by common accord.

The most remarkable fact about an observation of this kind is that totally blind insects should be able to recognize with such certainty the mishap that had befallen their tunnel, to come to an understanding among themselves, within a few moments, as to the work that had to be done, and then apply themselves each to its allotted task, and

reconstruct the wall in exactly the right place. Over and above the highly-developed tactile sense in the antennæ and palpi, over and above topochemical smell, it seems as though some photometric faculty must enter into this process. Although the sexless termites usually have no eyes, they are keenly sensitive to light, and most of them dislike it. When placed in a box with pieces of wood they hide under the *débris* directly the lid is raised. In the case of the partial destruction of a tunnel, the light which suddenly reaches the interior is the first stimulus to bring the brave little soldiers to the breach. When they foresee an attack, their first care is to attend to the defence. Then follows palpation with the antennæ. On completing their inspection, the soldiers give warning to the workers inside the tunnel and summon them to the rescue.

Eutermes matangensis (observed at Saigon) also constructs little cordons along trees. Bathellier has taken advantage of this fact to make an experiment comparable to my own, but with this difference, that near his site were some very aggressive black ants. A breach having been made, the ants rushed at the workers which appeared at the opening and bore off a certain number of them. A few moments later, when the soldiers had formed a circle of defence round the damaged part, the ants fell back along the whole line and forthwith ceased to attack the workers. Bathellier mentions another interesting detail. If one of the ants which were running along happened to get within some 2 centimetres of a soldier, she would retire without any attempt at resistance. This distance of 2 cm. probably indicates the range of the viscous liquid projected by the rostrum.

A third observation is concerned with *Eutermes lacustris*, of Ceylon (described in 1912). On November 22nd, 1910,

I encountered a nest of this species in a hollow tree (mangrove) at the edge of Lake Ambalangoda. I cut off with my hatchet the parts of the trunk occupied by the termites, put them into a bag and carried them to the bungalow. Some hundreds of soldiers and workers, as well as a large number of nymphs, were packed close to one another inside a wrinkle in the wood.

In the hope of obtaining winged adults, I had a little box made out of hard wood, covered it with a piece of glass which fitted into two grooves, and placed in it the pieces of wood which I had brought back from my excursion.

My installation was now complete. When I came back the following day I found that the table which bore the box had been invaded by ants (*Pheidologeton diversus*). As the glass was fairly loose, I at first expected disaster. But nothing of the sort had happened.

On receiving news of the danger,[1] the soldiers had formed up in line on the table, all round the box. A guard in close rank was also standing on the lid along the grooves which held the glass in place. The valiant little soldiers had been facing the enemy with their frontal horns and had not allowed a single ant to work her way in. The terrible *Pheidologeton* had turned their attention to a box of beetle larvæ and devoured its contents. The termite box was then placed on a table protected from ants and standing with its

[1]When disturbed, the soldiers, which are 4 millimetres long, completely blind, and characterized by their sepia brown heads and pale yellow abdomens, give signs of alarm (convulsive trembling) similar to those of *Eutermes monoceros*. The liquid secreted by the cephalic ampulla drips to the end of the frontal horn in the form of a transparent and very viscous drop. The worker, which is 4-4½ millimetres long, wears almost the same livery as the soldier. The nymphs, which are soft and plump and 7 millimetres long, have black eyes and dark brown wing stumps.

legs in water. Despite my precautions, the hatching of the nymphs could not be observed that year.[1]

Under natural conditions *Eutermes lacustris* insures herself against ants (like the species already mentioned) by making long brownish-coloured cordons (tunnels) along the trees out of scraps of wood and agglutinated dung. If the tree which bears the nest does not happen to supply wood of a suitable quality, the termites choose another and construct a tunnel along the trunks to enable them to come and go. Perched in a hollow tree or exposed to the open air, the nest of dark brown carton, with its hard outer covering, is so well protected by the soldiers, standing on a level with the openings, that the ants can obtain no access to the interior.

A fourth observation deals with *Eutermes monoceros* of Ceylon, sometimes known as the black termite. Its habits are different from those of the above species, for it constructs no tunnels, but goes instead on voyages of discovery which are very interesting to observe from our point of view. Constantly exposed to the attacks of the ants, the army is obliged to have a perfectly regulated watch on guard at the moment when it sets out on the march.

First of all a brief description of this termite's appearance will not come amiss. The soldier is nearly black, 4-5 millimetres long, and the protuberance of its occiput makes it look in profile (Plate XX) like a little horseman with a helmet on his head. Its thorax is concave like a saddle, but its abdomen is well rounded. The worker, of the same size as the soldier, is also black, while the larvæ (observed

[1] The adult sexual forms have since been found at Hantana by the Russian naturalist Oscar John, in a magnificent carton nest which stood in the fork of a tree branch, exposed to the open air. With Mr. John's permission I described them in *Spolia zeylanica*, 1914, and I here reproduce the photograph of the nest (See Plate XIX)

Nest of *Eutermes lacustris*, observed at Hantana (Ceylon).

(After a photograph by Mr. O. John.)

before the last moult) are still absolutely white. The pretty little queen represented in fig. 3 (18 millimetres long) was found at the bottom of a nest which filled the hollow part of a tree. So far as I know, the king has not yet been described.

The business on which *E. monoceros* sally out *en masse* consists in gathering lichens from bark to bring back to the nest as food for the larvæ, and possibly also for the royal couple.

The following observations deal with two colonies kept in captivity during the winter of 1910-11. The first nest, which was brought in on December 18th, was installed in the dry stem of a *Pandanus ceylonicus* (a large aquatic tree of the order Bromeliaceæ), $2\frac{1}{2}$ metres long, found on the edge of the lake at Ambalangoda. This stem was placed upright in a corner of the hut (laboratory), and from the first evening the termites went out in their usual manner. Four cocoa-trees, situated a few metres away, were visited in twelve days for the purpose of gathering lichens. The army that gathers in the spoils forms large black patches against the trunk, sometimes reaching as high as the first leaves. Each patch is divided into little groups, flanked by soldiers. Some of the workers in each group are occupied in gathering, while others receive the lichens from the labourers' mouths and collect them together in little masses. It is these last which can be seen in the returning army bearing their greyish-coloured parcels between their mandibles, while the others, much more numerous, simply return empty-handed.

On January 1st a second nest, round in shape and formed essentially of wood-carton, was brought to the laboratory and placed on the table some distance away from the other. The first day no movement was noticed. The following

night, the *Eutermes* of nest two took advantage of the absence of the army of nest one to invade the cavity of the *Pandanus* stem. This caused a battle when army one returned. The table was strewn with dead. The corpses, mostly workers, were more or less mutilated, and many of their legs and antennæ were amputated. The war lasted two days, after which peace was concluded and the two colonies combined to make one. Colony one, which probably had no queen, gradually abandoned the *Pandanus* stem and fused with colony two.

The army having become very large (owing to the fusion of the two armies), the expeditions were henceforth exceptionally interesting. Between January 5th and February 18th, 44 took place (one every evening). Eleven new cocoa-trees, some being 15-20 metres away, were exploited in turn. Sometimes a large squad would visit a plot of ground on the north side of the hut, apparently with the object of collecting humus.[1] The tracks which they followed across the front of the hut (marked in little black lines) were five in number altogether. They nearly always traversed the same road. The tracks outside varied a little, especially about their periphery, according to the position of the cocoa-trees that were visited. Owing to the fact that they were blind and guided exclusively by smell, the *Eutermes* wandered a long distance away on several occasions, before finding the right track. For instance, they acquired the habit of climbing up four poles fastened

[1] *E. monoceros*, which march in a line, leave behind them little black, elongated tracks (which are very distinct on a white road, for instance, or a distempered wall), and apparently serve to guide the army over its usual trail. As the intestines of these termites are filled with a black substance (see Bugnion, 'Le termite noir de Ceylon,' *Ann. Soc. ent. Fr.*, 1910), we may assume that the black marks were produced by a substance expelled from the rectum.

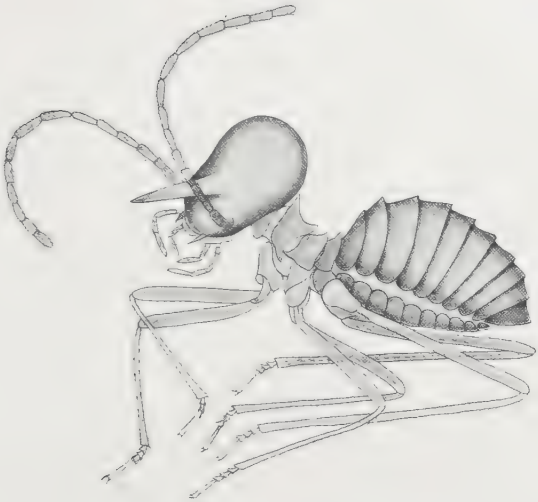

Fig. 1. Soldier × $12\frac{1}{2}$.

Fig. 2. Worker × 20.

Fig. 3. Queen
18 mm. × 3.

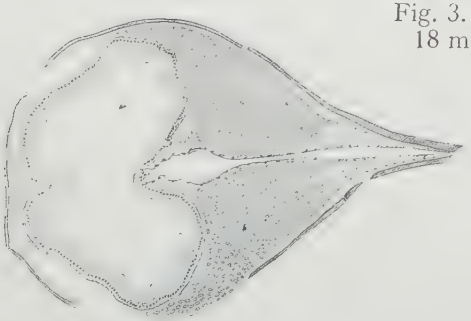

Fig. 4. Section of head of soldier, showing glandular ampulla × 50.

Eutermes monoceros.

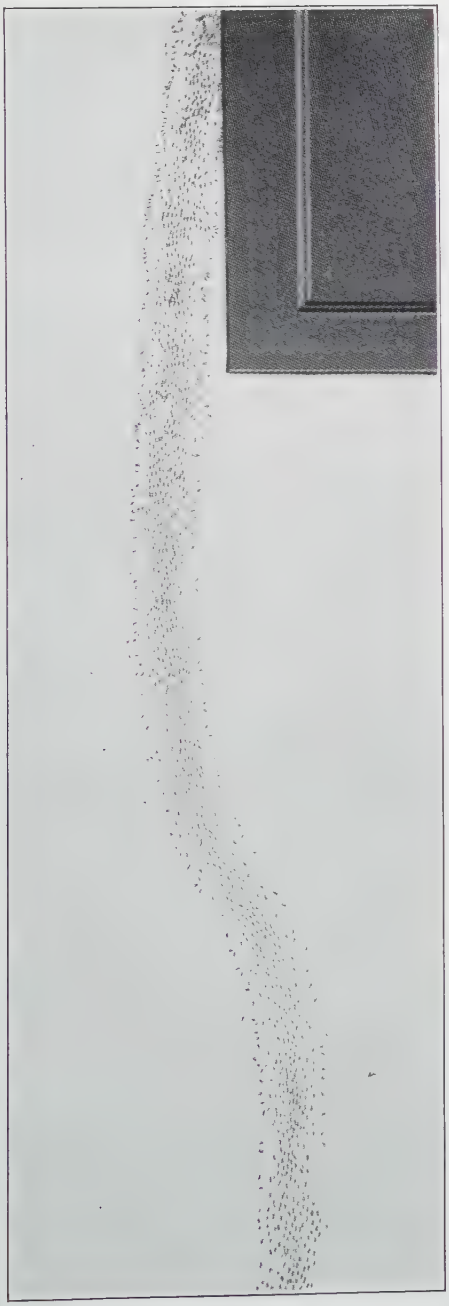

Fig. 1. Army setting out on the march across the wall of the laboratory at Seenigoda (Ceylon); flash-light photograph by C. Ferrière, Feb. 6th,

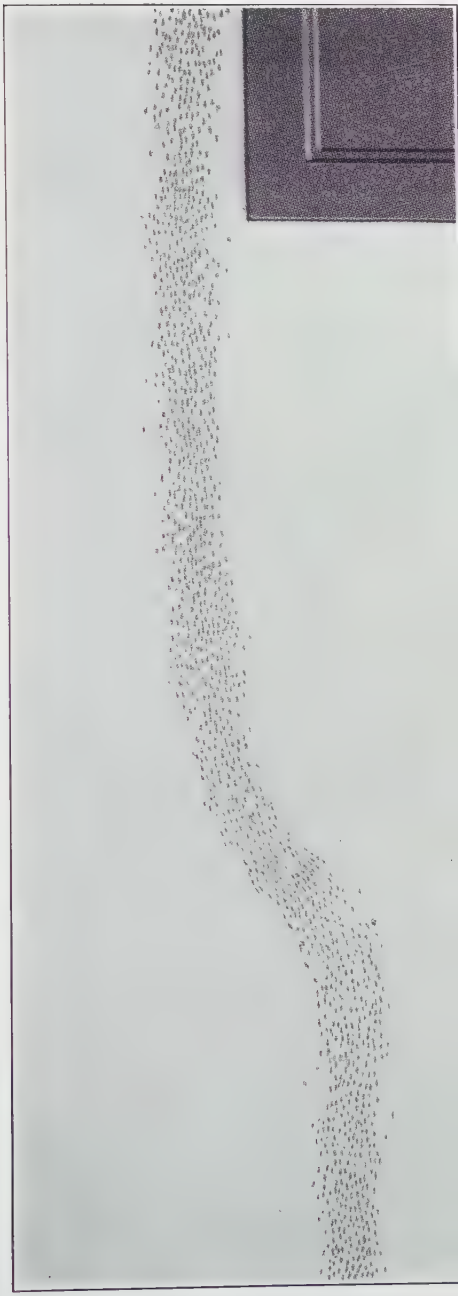

Fig. 2. Returning army photographed at 8 o'clock in the morning.

together in a bundle for a cooking pot to hang upon, and of passing down the other side instead of going straight along on the ground-level.

It was generally about 6 o'clock in the evening, just at sunset, when the *Eutermes* sallied out. When the sky was dark the exodus was sometimes observed to take place at 4-30 or 5 o'clock. At first the termites hesitated on their journey, and when they reached the base of the hut they would stray about from one side to the other for some time. As a rule two or three hours passed before the soldiers sent out as scouts discovered a tree likely to yield a good crop, and led the greater part of the troop after them. In every marching army a number of additional individuals (workers and soldiers) could be observed returning to the nest, especially at the moment of starting. A very lively to-and-fro movement thus provided an intelligence-service and established a connection between the marching army and the rest of the colony. Indication of the success or failure of the expedition is apparently given by the touch of the antennæ, and the alarm-signal, as several authors have noticed, is a trembling of the whole body (Zitterschläge).

The return, which generally began at dawn and lasted on an average for 4-5 hours, was completed as a rule about 7 o'clock. In a few cases (when termites had found a new cocoa-tree to exploit) the return journey began later and was prolonged to the exceptionally late hour of eleven or twelve. The heat of the sun on the front of the hut, facing east, then troubled the termites and made them walk more quickly.

Our photographs, one taken by flash-light (the army setting out) the other by daylight (army returning), show the guard of soldiers drawn up in two rows, with the long file of workers between them. The soldiers, which stand

motionless to left and right, with their heads all turned in an outward direction in view of possible ant-attacks, are especially numerous at the moment when the termites set out.

The number of the out-going army, counted from enlarged photographs (flashlight) are estimated at 232-623 to a distance of 32 centimetres, or 806-1917 to a metre. If we take 1,000 per metre as an average figure, the total for the whole termite army, marching for five hours at the rate of one metre per minute, is 300,000. The soldiers on guard, counted from one of the photographs, amounted to 80 on the left and 51 on the right, for a distance of 55 centimetres, which gives 146 and 92 to a metre, or 238 altogether. One day when the returning army was harassed by ants (*Pheidologeton*) I counted along the basement of the hut, over a distance of $3\frac{1}{2}$ metres, a row of 281 soldiers, facing the enemy and covering the retreat of the lichen-laden workers, which walked on the side of the wall, sheltered from the aggressors.

In short, the above observations go to prove that the chief aim of the nocturnal expeditions of *E. monoceros* is the gathering of lichens. I have always noticed that under certain circumstances *E. monoceros* also gathers leaf-*débris*. It may also be mentioned that numerous groups of termites love to linger on the black earth, from which they seem to be extracting some substance. Possibly the contents of the intestines owe their distinctive black colour to some matter drawn from the humus. In conclusion, I can state that *E. monoceros*, unlike *E. matangensis* and *lacustris*, which both attack wood, is absolutely harmless. The two enormous colonies which inhabited my laboratory for 79 days deserved no reproach in this respect.

Some of the cocoa-trees exploited by my *Eutermes* bore

Œcophylla nests in their fronds. As the ants continued coming and going along the trunk both day and night, the arrival of the termites was naturally the occasion of a death struggle. This enabled me to observe the tactics of the soldier and the rôle of its ampulla much better than I had done in the previous years.

The *Œcophylla*, despite its agility and its three times greater size, is put out of action in an instant. Moreover, the *Eutermes*, provided that their numbers are sufficient, and also that they are already on their guard and have had time to organize their defence, nearly always emerge victorious from these combats. The army hesitates at first, when the ants bar its way, and perhaps remains for several hours at the foot of the tree. The observer thinks at first that this means defeat. But if he watches the opening stages of the struggle one evening and returns at dawn the next day to the same cocoa-tree, he nearly always finds the termites grouped in large patches on the surface of the bark, calmly occupied in gathering lichens.

Terrible as they seem, once these ants are overcome by the frontal squirts of the little soldiers, they are obliged to leave the field to the *Eutermes* for the time being.

3 The *Capritermes* (soldiers) have mandibles of a peculiar shape, twisted like the horns of a goat in order to help them in leaping. When bent against the ground, these organs act like a spring and enable the termite to project its body into the air. The insect comes back to the ground 20-30 centimetres away, and manages to escape from its enemies by jumping from side to side. I am unable to state, however (as my observations are still incomplete) whether the curious catapult used by *Capritermes* is specially intended to save it from the ants.

4 Other facts of interest concern the genera *Coptotermes*

and *Arrhinotermes*. *Coptotermes* Silvestri (latex-termite) has one great peculiarity: the soldier (*C. ceylonicus* Holm), which is closely connected with *C. travians* Hav. of Malacca, $4\frac{1}{2}$ millimetres long, is distinguished from the worker by its sickle-shaped mandibles and its milk-white abdomen. When molested it emits a little drop like india-rubber latex which suddenly appears above the labrum and remains for some time before it rolls down. Examination under a microscope makes it plain that this liquid trickles through a round opening (frontal pore) situated behind the epistoma. The gland which produces this secretion is not limited to the head, like that of *Eutermes*, but also occupies a large part of the thorax and abdomen (see the section drawn in Plate XXII).

This latex is an effective means of defence against ants; it sticks their mandibles and antennæ together and renders them harmless. But, curiously enough, the termite itself often appears to be encumbered by its latex. Nature would seem to have given these insects a defensive weapon which paralyses themselves; though if a few soldiers out of the enormous population of the termitary are put out of action, they can be quickly replaced.

During an excursion which I made in the company of Prof. Escherich, on February 3rd, I observed a *Coptotermes ceylonicus* nest at Ambalangoda in the trunk of a tree (*Anacardium occidentale*). When the tree, which was hollow inside, had been cleft with a hatchet, we saw that the nest occupied the cavity of the trunk to a height of about 70 centimetres, and extended below among the roots and the soil. Above the cavity, in addition to the ligneous layers which surrounded it in concentric formation, there was a compact mass, dark-brown in colour, formed of agglutinated dung, and, farther inside, a system of brown, friable

Fig. 1. Winged sexual form × $8\frac{1}{2}$.

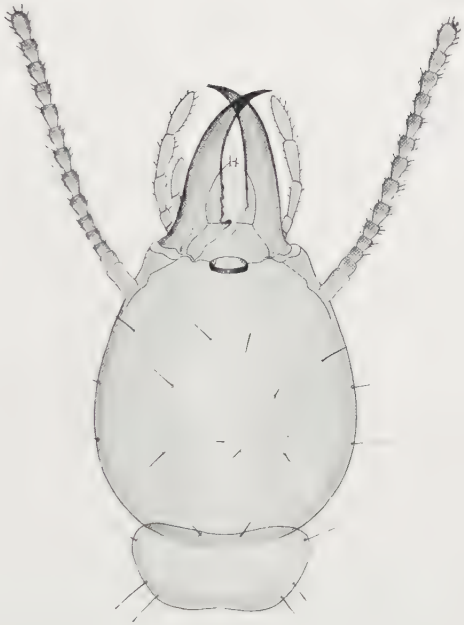

Fig. 2. Head of soldier showing frontal pore × 24.

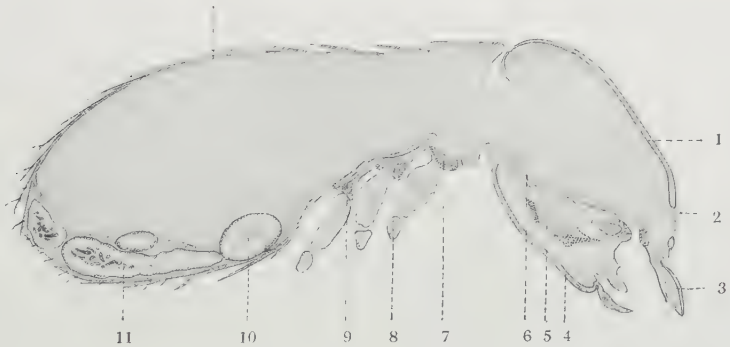

Fig. 3. Longitudinal section of soldier × 26.

1 **Latex pouch.** 2 Frontal pore. 3 Labrum. 4 **Basilary plate.**
5 Sub-oesophageal ganglion. 6 Oesophagus. 7, 8, 9 Thoracic ganglia.
10 Stomach. 11 Posterior intestine full of **Trichonymphides.**
(*Drawing by N. Popoff.*)

Coptotermes ceylonicus.

flakes made of wood-carton. The rôle of the compact mass is certainly to keep the upper part of the cavity hermetically sealed and so prevent ants from entering.

Hundreds of workers could be seen everywhere; also soldiers ready to bite, and mostly showing their drop of latex at the frontal pore. Deep within, we also found a large number of white, newly-hatched larvæ, walking slowly among the roots. In the hope of finding the queen, we began to prick eagerly at the foot of the tree, but without success. The honoured matron remained absolutely inaccessible on this occasion.

Arrhinotermes, which is akin to the above genus, also has a frontal pore and a glandular pouch extending behind to the end of the abdomen. One species of this genus (*A. flavus* Bug.) was discovered on January 2nd, 1910, on the borders of Lake Ambalangoda, under the bark of a dead tree. Other nests containing imagines were found, in the following years, on the borders of the same lake, in the hollow stems of *Pandanus ceylonicus* (a large aquatic plant of the order Bromeliaceæ), or under the bark of the mangrove (*Rhizophora mucronata*). These constructions were completed and protected by dark-brown carton. The soldier is 6 millimetres long, flat and elongated in shape, wears a yellow uniform, and emits a transparent, lemon-coloured liquid when alarmed. The larvæ here found came out of the egg with two little membranous wings, which were unusual in being attached to the pronotum. The lemon-coloured liquid which escapes from the frontal pore is a defensive measure, like the latex of *Coptotermes*, specially adapted to warfare with the ants.

5 *Calotermes* (κᾶλον, wood) differs from the higher termites in having no clearly marked worker caste. The larvæ, which form the largest proportion of the colony,

fulfil the function of the workers in carving wood, and perhaps in feeding the young. They are apparently capable of turning into nymphs, some of which produce males, others females. A certain number of these larvæ may, however, remain in the neuter (asexual) state, and represent a half-formed worker caste. The soldiers, relatively few in number, are distinguished by their larger size, their big yellowish-brown heads, their strong mandibles with multifarious teeth, and the presence of two little facet eyes, with no pigment, but clearly recognizable under the microscope. The egg-laying females, being scarcely larger than the nymphs, supply only a small number of eggs, but to compensate for this there are several of them in each colony.

Most authors agree in regarding *Calotermes* as a lower and primitive termite group. The structure of the soldiers, however, indicates a special differentiation, already highly advanced in this caste. Like the xylophagous beetles, *Calotermes* carves narrow galleries in dead wood, and even in living wood, and is usually confined for life to the interior. Larger cavities, usually hollowed out of the hardest nodes, are specially reserved for the hatching of eggs and the rearing of young larvæ.

These termites have little skill as masons and are equally incapable of making carton, but they have special defence measures of their own, chiefly intended to preserve them from ants. These measures are of two kinds. The first consists in padding the outer part of the gallery with lumps of mud mixed with sawdust. The second—a hastier expedient—is merely the posting of a soldier at the entrance of the gallery, with its large head and strong mandibles turned, of course, towards the exterior. The head-formation characteristic of certain species (soldiers) seems to be specially adapted for this purpose. By way of illustration I

Fig. 1. Soldier × 13.

Fig. 2. Larva, 4½ mm. × 15.

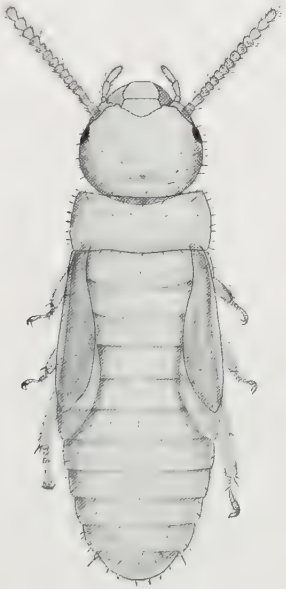

Fig. 3. Nymph, 5 mm. × 15.

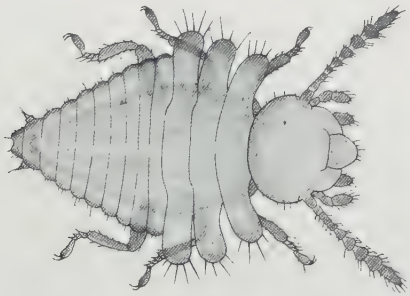

Fig. 4. Larva, 1½ mm. with thoracic expansions × 21.

Calotermes dilatatus.

may mention the forehead of *Calotermes diltaatus* Bug., which has an abrupt slope (See Plate XXIII), reminiscent of the conformation of certain Bostrichus.[1]

My studies have been mainly concerned with *Calotermes Greeni* Desneux. Among others, an observation which I made on January 23rd, 1910, is worthy of mention. I had come that day to the shore of an island in Lake Ambalangoda, which was almost deserted and seemed a very promising hunting-ground; and there I happened to catch sight of an *Anacardium occidentale* (a tree bearing edible cashew nuts, originally from Brazil), with a fairly large, half-dried branch, which appeared to be infested with termites. Having sawn off this branch, about 2 metres above the ground, I saw that it contained galleries stuffed with lumps of brown dung and sawdust, and found within it a number of *Cal. Greeni* larvæ.

These larvæ (in this particular case 4-6½ millimetres long), characterized by their slow movements and plump bodies, have yellowish-white (sulphur-coloured) front parts and reddish-brown abdomens streaked with pulp (formed essentially of Trichonymphids) which accumulates in the highly dilated cæcum. The white spots are due to the oil bodies which are scattered about in various places above the intestines. The soldier (I saw only one on this occasion) is noticeable by reason of its large size (10-11½ millimetres),

[1] In this connection we may recall that the male of these insects, *Hylesinus*, *Scolytus*, take care to keep on guard at the entrance to their gallery, which is barred by their almost vertical forehead, whilst the egg-laying female is busy within. In *Calotermes* this rôle of guardian has devolved on the soldiers.

Certain ants of the sub-genus *Colobopsis* also have vertically truncated heads, in the soldier and the female, while the male and the worker have heads of the ordinary shape. The soldiers, acting as janitors, hermetically close the door of the nest; the queen-mother does the same. These nests are hollowed out in bamboos and galls, or in dry or broken branches. See Part V, Chapter V [Forel].

its big, yellowish-brown head, and its powerful, multidentate mandibles.

On February 7th, a second branch, several metres long, containing a populous *C. Greeni* colony, was removed from the same tree, and after being divided into several fragments was placed on board and taken to the bungalow. But a disappointment awaited me. I was imprudent enough to lay down the fragments of wood with their termites on a lawn and go away to lunch. I came back in half an hour and cut open the pieces with a hatchet, only to find my precious larvæ mangled and my handsome soldiers beheaded. Reduced to the condition of live heads, these soldiers were still trying to bite with their great mandibles, but they were totally bereft of bodies. Countless little ants (*Pheidologeton diversus*), hidden in the turf, had profited by my absence to penetrate into the galleries and devour their inhabitants.

These details, which I report for the benefit of naturalists exploring in tropical countries, show the dangers to which the termites are exposed when some clumsy interference suddenly lays open the galleries which they usually keep hermetically sealed. Assailed from behind and unable to turn round in their over-narrow passages, the hapless soldiers had been incapable of defending themselves.

Among the ants which attack termites most fiercely we have still to mention those described by Maxwell Lefroy in his *Indian Insect Life*, 1909, p. 226 and 228; *Lobopelta diminuta* Sm. (Ponerine), *Monomorium Salomonis* Lin., and *Solenopsis geminata* Fabr. (Myrmicine). According to Rothney, the last two species (which have stings like *Pheidologeton* and the Myrmicines in general) are utilized by the natives of Madras to destroy termites in the goods-warehouses. An excellent work, *Les Termites*, recently

Fig. 1. Winged sexual form × 7.

Fig. 2. Head and thorax of soldier × 14.

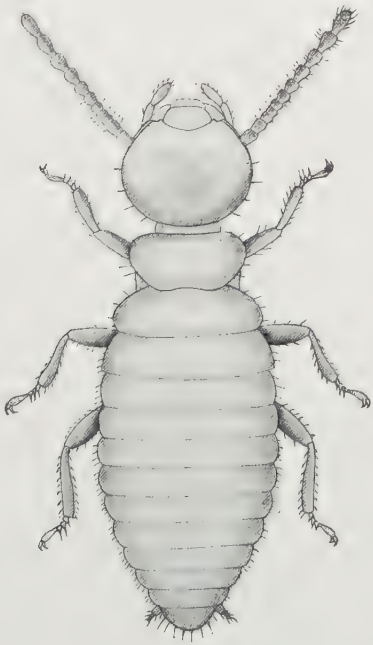

Fig. 3. Larva, 3 mm. long × 20.

Calotermes Greeni.

published by E. Hegh, an engineer attached to the Colonial Ministry at Brussels, contains some interesting details as to wars between ants and termites observed in tropical Africa.

The bitterest enemies of the termites belong chiefly to two sub-families of ants, the *Ponerinæ* and *Dorylinæ*.

Megaponera fœtens, a brown ant about 1 centimetre long, makes veritable raids upon the termites, which have been described by the various authors, notably by H. Prell in Usambara (German East Africa). He tells us that when a piece of land containing termitaries is discovered by ants, the invading army splits up and pours into the holes or cracks leading to the galleries they wish to invade. Each ant brings one or two termites up to the surface and then returns to the galleries to draw forth more victims. The raid continues until every ant has taken half a dozen prisoners, which struggle feebly on the ground in a mutilated condition; after which each marauder picks up three or four termites—an easy burden for her—falls into her rank again and returns with the column to the nest.

In a case observed in 1910 a *Megaponera fœtens* army was coming back through the forest after plundering a nest of *Termes bellicosus* (a large African termite, notorious for its bite). Every ant bore in her mandibles a few slain enemies, either three or four workers, or two large soldiers, each weighing more than twice as much as their bearer. The army spread over a space about 10 centimetres wide by 1½ millimetres long, and stridulated perpetually as it marched.

Carpenter, who studied the same ants in the south-west of Lake Victoria, says that their columns, 50-500 strong, never carry any other prey than termites. According to Ghesquière, who has studied *Megaponera* in the Belgian Congo, the combat within the galleries lasts but a very

short time. On their return, more than 80 per cent. of the ants carry prey, termite soldiers, workers, and nymphs; the number of wounded ants which drag painfully along in the rear of the column may be estimated at 4 or 5 per cent. of the whole.

Arnold gives a list of other Ponerine ants which prey upon termites and are consequently very useful: *Paltothyreus tarsatus* (Fabricius), *Euponera sennaarensis* (Mayr), and *Leptothorax Schwabi* (Forel). The *Dorylinæ* family also include carnivorous ants, excessively predatory and commonly known as visiting or nomad ants (the English Driver or Devil ants). In the Congo they form huge armies and devour all animal substances lying in their path, including quantities of termites.

In New Orleans (Louisiana), *Iridomyrmex humilis* (Mayr), the Argentine ant, is a great enemy of the termites, more especially at the moment of swarming. *Iridomyrmex sanguineus* (Forel) behaves similarly in North Australia. This species penetrates the termite nest by carving holes in their walls, and wages such bitter warfare with the termites of South Queensland that 80 per cent. of the nests of *Drepanotermes Silvestrii* and *Hamitermes perplexus*, according to G. H. Hill's estimate, are gradually invaded and afterwards permanently occupied by these *Iridomyrmex*.

The Genesis of Instincts

The war between ants and termites is of paramount interest in connection with the genesis of instincts. In fact it is to this war, this ceaseless struggle, that the instincts of these insects may be directly related, more especially the instincts of the termites, which, being less well armed, have been obliged to apply more ingenuity to the task of defending themselves.

If it be true that the origin of instincts was lighted by a ray of intelligence, a reasoned and conscious form of action,[1] and that these reasoned actions, many times repeated, become more or less automatic habits; if we assume, moreover, that every action useful for the conservation of the species tends to leave a durable impression on the brain, and accordingly to become hereditary, the genesis of instinctive activity unfolds itself clearly and convincingly before our minds.

In opposition to Weismann, who refused to admit the transmission of acquired characters (psychical or physical), but in agreement with Semon, Claparède, Piéron, Hachet-Souplet, Forel, and, in a general way, with most modern psychologists, I unhesitatingly maintain that the hereditary transmission of newly-acquired instincts is a proven and henceforth incontrovertible fact.

If it were not so, how could we conceive the origin of instincts and the improvements they have undergone in the course of the ages? Nature goes her way and fulfils her evolution without troubling about our human theories. The over-narrow frame in which Weismann tried to enclose her has broken down of its own accord in the presence of real facts.

The study of termites is very instructive in this respect. Among the present-day termites are some very primitive types (*Mastotermes*, *Termopsis*, *Hodotermes*, *Calotermes*), side

[1]Human reason and animal instinct have long been regarded as having nothing in common. But all psychological naturalists recognize to-day with Darwin, Perrier, Romanes, Bouvier, etc., that we must of necessity assume intelligent processes at the beginnings of instincts, which are only 'hereditary habits.' *a kind of automatic reason*, examples of which are not lacking even in man. (This remark is taken from Boule, *Les hommes fossiles*, p. 297. E.T., 1922, *Fossil Man*). Prof. A. Forel, in *Gehirn und Seele*, 1894, also put forward the same view.

by side with more recent and highly-perfected forms, and hence we have only to observe the habits and customs of each species in order to follow step by step the evolution of instincts and their ever-increasing complexity.

In the following account we have to distinguish between three categories of instincts:

A Instincts connected with defensive measures borrowed from Nature;

B Instincts connected with anatomical structure, or, in other words, the defensive organs of our insects;

C Instincts resulting from mental dispositions which, being of use in the conservation of the species, have become automatic.

Evolution of Instincts Connected with Defensive Measures Borrowed from Nature

Let us continue the study which we began above, proceeding this time in the opposite direction. Starting from the bottom of the ladder (*Termopsis*, *Calotermes*) we shall gradually ascend to the higher genera (*Eutermes*, *Termes*), characterized by instincts of a more complex and highly-perfected character.

Let us imagine that a primitive termite has installed its gallery in a tree trunk, and finds itself constantly menaced by very aggressive ants, which try to penetrate to the interior with the design of carrying off larvæ. Obeying a perfectly natural impulse, it will face the enemy at the entrance to its burrow, with threatening mandibles, ready to bite. The termites entrusted with the defence are no doubt already the strongest and most courageous; when gradually differentiated and armed with more highly-developed mandibles, they will soon form a soldier-caste.

But this rôle of sentinel is in the long run irksome and

very painful, leaving the termite no respite. And we may easily conceive our insect, as it becomes more and more obsessed by the ant which is its torment, inventing for itself a means of protection. A very simple plan lies directly open to it. It consists in this, that instead of throwing sawdust outside, the termite whose duty it is to mount guard will henceforth allow the wood-*débris* to accumulate. This sawdust, when carefully heaped up and compressed, forms a compact cork which closes the gallery and prevents any intruders from entering.

Protected against their enemies by these sawdust corks (sometimes by pellets formed of sawdust mixed with dung), the termites which have reached this stage may now, without fear of being devoured, broaden their galleries in the deepest parts, and there lay their eggs and rear their young larvæ in perfect safety.

Here we behold the genesis of an instinct. A very simple intelligent action, the heaping of sawdust, sufficed to make this means of protection become henceforth habitual. Being of use in the conservation of the species, the heaping of sawdust has gradually become a habit by the action of natural selection, and after some time this habit gives rise to an automatic activity, that is, a new instinct, transmitted from one generation to another by the laws of heredity.

This, surely, is the phase of instinctive life reached by *Calotermes* at the present time, the termite which installs its galleries inside solid wood.

Satisfied, apparently, by the conditions of life in which it finds itself, the present-day *Calotermes* does not for the moment seek to perfect its habits. This, in the eyes of biologists, is a primitive termite, which, apart from the differentiation of a soldier-caste with strong mandibles, has undergone very little modification up to the present day.

Let us take one step farther forward. It is easy to imagine a wood-carving termite which, having broadened its gallery in view of the multiplication of its family, and having accumulated sawdust, as a protective measure, in the outer part, observes that this sawdust is falling away and racks its little brain for a means of avoiding this accident. It is only a puny insect, but, taught by experience, it has a few conscious ideas, a few intuitions which cause it to reflect.

According to our modern ideas, the presence of fixed instincts is in no way incompatible with a few gleams of intelligence, with certain reflective and conscious actions which unite with the instincts already formed and enable them to be further perfected. And so, since the wood-chewing termite has salivary glands, why should it not use the liquid with which they supply it? The way to do this is soon discovered. Bedewing the wood-fragments with saliva, our little labourer makes the mixture into a kind of paste which hardens as it dries; it can then use this paste to make walls, pillars and partitions.[1]

The wood-carton industry, which plays so large a part in the biology of *Coptotermes*, *Arrhinotermes*, and *Eutermes*, may possibly be explained in this manner. The substance known as wood-carton lends itself to all manner of modifications. In this case, for instance, when the termites are installed in a hollow tree, the wood-paste is used for making a covering and building an operculum. The first essential is that the cavities, apart from the little aperture protected by the soldiers, should be closed, so that the ants, in particular, cannot enter.

[1]Dr. A. Imms observed a termite which, though belonging to a very primitive genus, used a mixture of sawdust and saliva to stop up the crack in the wood. This creature is *Archotermopsis Wroughtoni*, a species which carves its galleries in the dead trunks of conifers in the Himalayan region. (See *Phil. Trans.*, Series B, Vol. 209, 1916, p. 126).

Under other circumstances the nest of carton-wood, flaky in structure and brown in colour, is exposed to the open air; hung on a bush or placed between two forked branches, Carton nests suspended from trees, built by *Eutermes lacustris*, have been observed in Ceylon by O. John (Plate XIX) and myself. They are oblong or oval in shape and surrounded by a solid covering, intended as a precaution against the attacks of the ants. The nests of this type, known as *arboricolous*, are especially common in Borneo, Madagascar and Australia.

The greyish cordons (tunnels) constructed by certain *Eutermes* vertically along trees and sometimes along walls constitute a variation in the carton industry. The first character which differentiates these cordons is the admixture of grains of earth with wood-*debris;* a second special feature is the replacement of the saliva by a yellow liquid expelled from the rectum for the purpose of cementing the walls, which are consequently much more friable.

The aim of *Eutermes* in constructing tunnels along the trunks is manifestly to permit the inhabitants of the nest to go in search of victuals[1] without being constantly molested by ants. Moreover, it is clear that, should part of the tunnel be destroyed (as in the experiment related above), the soldier-termites have no thought of resisting man (an enormous animal of which they can form no notion whatever), but only of *guarding themselves against ants;* and for this purpose alone they establish a protective ring round the breach and keep their frontal horns thrust outward while the whole work of reconstruction is in progress.

From the wood-carton industry we pass naturally to the

[1]The victuals, in this particular case, may be the sweet liquid which oozes from the terminal bud of the cocoa-tree, or perhaps the pollen which is to be found on the flowers.

art of constructing masonry with mortar made of earth and saliva—an art which is especially well developed among the higher termites (*Termes*) and intimately connected with their way of living. Here again, we can easily picture to ourselves how the masonry art, practised at first on a humble scale with a view to propping up walls or consolidating tunnels, has been gradually perfected in the course of ages.

Certain *Coptotermes* observed in Australia are peculiar in that their dome-shaped nest comprises an internal part made of wood-carton and occupied by the termites, and an external covering formed of grains of earth glued together, which serves to protect the termite-mound as a whole. Confining themselves at first to plastering trees and constructing tunnels, the ingenious labourers gradually learnt to build walls and cement chambers. After various attempts they discovered how to build these domes with that inexpugnable solidity which is a source of astonishment to travellers in tropical regions.[1]

Last of all, in addition to the arts of building and of forming closed chambers, came the crowning achievement in the evolution of instincts—the astounding fungus-growing industry. Designed for feeding the young larvæ and the king and queen, and perhaps, to a certain extent, the winged individuals, the cultivation of mushrooms is apparently derived from the gathering of moulds which grow on rotten wood. As the new-born larvæ are too weak to carve wood and feed upon it, it is extremely probable that learning to plant 'gardens' the primitive termites fed their

[1]The largest known termite-mounds (found in Africa) measure no less than 6 metres in height by 3 or 4 in diameter at the base. If we remember that in order to build such edifices the worker-termites have brought thither, one by one, the little grains of earth which serve as rubble, and have bedewed them one by one with their saliva, we shall realize the truly astounding nature of such an achievement.

young with moulds and lichens. It is possible, moreover, that fortuitous circumstances may have caused the sowing of fungus-spores brought from the outer world.

Imagine a termite (worker) busy carving wood in the forest, turning its attention to one of the agarics found on tree-stumps. Assume further that certain conidia, capable of germinating, mix with the wood-paste contained in its intestines. The result can be readily foreseen. Mycelium producing hyphæ would develop on the heaps of refuse inside the termitary, and the termites would find in these hyphæ a congenial food. After several experiences of this kind they would discover fungus-growing, and would learn to plant gardens.

Whatever its origin may be, the cultivation of fungi is of prime importance to the colony. This alone enables the higher termites to maintain queens with enormous ovaries, capable of laying thousands of eggs a day, and this alone assures the successful rearing day after day of thousands of larvæ.

To sum up the above observations in a few words, we may pass up the termite scale from the lowest to the highest and distinguish various degrees in the growth of their industries, and, consequently, in the evolution of their instincts:

1st degree. Heaping of wood-sawdust in the outer part of the galleries. More or less compact sausage-shaped pellets, formed of sawdust and dung, intended for stopping up the exit-holes (*Calotermes*, *Termopsis*);

2nd degree. Agglutination of wood-*débris* by means of the saliva or the liquid contained in the rectum, in order to form tunnels, protective partitions and entirely closed nests. Wood-carton industry in general (*Coptotermes*, *Arrhinotermes*, *Eutermes*);

3rd degree. Art of building with mortar formed of earth-grains and saliva. Gradual improvement of design, from simple incrustations of earth to the most perfect termite-mounds (*Coptotermes*, *Termes*);

4th degree. Cultivation of fungi. Further and further perfection of the art among fungus-growing termites. (*Termes*).

The various degrees observed in the utilization of natural elements (wood-*débris*, earth-grains, fungi) can be explained, as we see, by a small number of very simple rational and conscious acts, which proved to be useful for the conservation of the species and were accordingly transformed gradually into habits and finally into hereditary instincts.

It may also be laid down that the various instincts connected with the utilization of natural elements are all the result of *adaptation to circumstances*; in other words, their basis is the incessant warfare between ants and termites, which caused the weaker insects to set up a *vast protective system* against the stronger.

Represented at first by simple galleries closed at their free end by sawdust stoppers, this protective system must have been perfected in the course of the ages,[1] and its final triumph is the dome-shaped termitary, the *ne plus ultra* of termite industry.

[1]N. Holmgren (*Termitenstudien* II, 1911, pp. 14-33), after comparing the wings of the present-day Australian *Mastotermes* with those of the Blattids concludes from his study that the termites are related to the Protoblattoids and probably derived from them.

As the Protoblattoids died out during the Permian, the first termites must have appeared during the Mesozoic Age. Admittedly, these ancestral types have not yet been found. The oldest termites known belong to the Upper Eocene. But it is a peculiarly interesting fact that the termites of the Eocene are closely connected with g. *Mastotermes*. Kurt von Rosen has described under the name of *Mast. bournemouthensis* a termite of the Bartoman (upper Eocene) of Bournemouth, which, though quite distinct, yet resembles *Mast. darwinensis* (the present-day species) in many respects.

Instincts in Connection with the Anatomical Structure and the Evolution of Defensive Organs

Though it is relatively easy to observe the gradual improvement of protective measures borrowed from the external world, the evolution of defensive organs is, on the contrary, somewhat difficult to explain. We will nevertheless attempt to establish a few landmarks.

In the first place I append a list of organs, which cannot claim to be complete, but which does at least include those which I have had occasion to see at work.

1 The shape and power of the mandibles, peculiar to the soldiers;

2 The size of the head observed in the soldier, its more strongly chitinous character, the welding of its ventral

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Other fossil termites discovered in the middle Oligocene of the Isle of Wight also belong to g. *Mastotermes*, and constitute two species (*M. anglicus* and *Batheri*) described by von Rosen. A fourth *Mastotermes* (*croaticus* von Rosen) has been recognized by Holmgren and von Rosen among the fossils of the Lower Miocene of Radoboj in Croatia. The genus *Termopsis* Heer, is also an ancient form found in the fossil state in the Tertiary, represented at the present day by four species: *T. Wroughtoni* Desn. of Kashmir, *T. angusticollis* Hagen of the mountains of California, *T. Sjöstedti* of Tonkin, *T. japonicus* of Japan. One species *Archotermopsis Tornquisti* von Rosen has been found in the Baltic amber.

The ants are perhaps not quite so old as the termites. But it has been proved that several existing genera (*Formica*, *Polyergus*, *Ponera*, *Myrmica*) date back to the Miocene (Middle Tertiary). As the duration of the Tertiary period has been estimated by competent geologists at 1,500,000-2,500,000 years, that of the Quaternary at 12,500 years up to the present day, it is clear that the two groups of insects with which we are concerned (ants and termites) have had a very long time in which to adapt themselves to each other. See O. Heer, *Die Insektenfauna der Tertiärgebilde von Oeningen und Radoboj*, Leipzig, 1849, II, pp. 22 and 101; *Die Urwelt der Schweiz*, Zurich, 1865, p. 387; Handlirsch, *Die fossilen Insekten und die Phylogenie der rezenten Formen*, Leipzig, 1908; Kurt von Rosen, *Die fossilen Termiten* (Transact. 2nd Entom. Congress, 1912, p. 318); Edm. Perrier, *The Earth before History*, London, 1924; Boule, *Les hommes fossiles*, Paris, 1921, p. 30 (E.T. *Fossil Man*, 1922).

wall (*basilary*), and, in a general way, the solidarity of its capsule;[1]

3 The power of emitting a rattling noise (alarm-signal) by striking the ventral wall of the head against wood, dry leaves, etc., in connection with the solidity of the cranial capsule (soldiers of *Hodotermes* and certain *Termes*);

4 The capacity of producing convulsive tremors (German Zitterschläge) which also serve as alarm-signals, in connection with a special adaptation of the nervous system (soldiers of *Archotermopsis*, according to Imms, and of various *Eutermes*);

5 The presence in certain types (soldiers of g. *Eutermes*) of a frontal horn and a cephalic gland secreting a viscous liquid designed to adhere to the ant's limbs;

6 The presence of a frontal pore and a latex gland playing practically the same rôle (soldiers of the genera *Coptotermes* and *Arrhinotermes*);

7 Mandibles developed for the purpose of leaping (soldiers of g. *Capritermes*);

8 The enormous fertility of the queens (*e.g.*, *Termes*);

9 In a general way, the differentiation of castes and the resulting division of labour.

I shall shortly say something about the differentiation of workers and soldiers. Before going further, however, I should like to enumerate the instincts which form my third category, according to the classification adopted. It will be best to mention one after the other the special instincts peculiar to the termites, and to deal last of all with the differentiation of castes and the evolution of instincts in general.

[1] With insects in general, the size of the head is in direct relation to the development of the masticatory muscles; hence it is easy to understand why the cranial capsule of the soldier usually presents much greater dimensions

INSTINCTS RESULTING FROM MENTAL DISPOSITIONS WHICH HAVE PROVED USEFUL FOR THE CONSERVATION OF THE SPECIES AND HAVE GRADUALLY BECOME AUTOMATIC.

1 The tenacity of the soldier in its defensive actions, individual and collective.

2 The scout-duties carried out by the soldiers, the organization of expeditions of discovery (*Hodotermes*, *Eutermes monoceros*, *Termes convulsionarius* of India and Ceylon, *Termes Lilljeborgi* of tropical Africa);

3 The unwearying activity of the worker in carving wood, gathering lichens, stumps of stubble, etc., for the building of fungus-gardens and for works of construction or eventual reconstruction;

4 The organization and protection of the swarm by soldiers and workers entrusted with this task;

5 In the sexual forms: the swarm, nuptial promenade, mating and foundation of new nests;

6 The protection of the royal couple (the incarceration observed in the higher termites); the feeding of the queen and king with fungi and saliva (by the workers and soldier-nurses);

7 The maternal care (licking, transport to the fungus-gardens) bestowed by the sexless forms upon the eggs;

8 The care bestowed upon the larvæ and nymphs, their removal to shelter in case of alarm (comparable to the rescue of the larvæ and cocoons observed in ants).

DIFFERENTIATION OF WORKERS AND SOLDIERS.

In the conformation of the head, and more particularly in the structure of the mouth-pieces, the worker termite resembles the sexual forms, but, judging by all that we can see, it has been differentiated from the primitive winged type by a series of very gradual modifications. The atrophy

of the genital glands, the disappearance of the eyes, the arrested development of the wings (in connection with the suppression of the last moult) are sufficient to account for the passage from one form to the other.

The principal purpose of the differentiation of castes being division of labour, it is easy to understand why the non-dome-constructing termites, which dig galleries in tree trunks (*Archotermopsis*, *Calotermes*) have not, up to the present day, reached the stage of differentiating their workers.

The origin of the soldier raises more thorny and more complex questions. If the only points at issue were a modification of the mandibles, a lengthening of the head, the welding of the basilary plate and a more pronounced chitinization of the cephalic capsule, the problem before us would still be fairly simple. The process would consist, in brief, of gradual modifications comparable to those which gave rise to the workers. But we are confronted by something quite different. The soldier, in all the genera which possess it, really constitutes a type apart, without any known intermediary. How, for example, must we interpret the presence of the frontal horn in *Eutermes*, when there is no intermediate ancestral type? And who can explain the origin of the latex gland in *Coptotermes* or *Arrhinotermes*? How are we to conceive that capricious differentiation by virtue of which the soldier's head becomes very hard, arms itself with powerful mandibles, and, in a word, acquires the highly specialized structure which is its characteristic, whereas the posterior part of the body, which remains very vulnerable, exposes our insect to the worst dangers? Ought we to suppose that the differentiation of the soldier took place at an epoch (the *Calotermes* stage) when the termite stood on watch at the entrance to its gallery, and had scarcely any occasion to expose its abdomen uncovered?

An explanation of this kind is adequate for the crustacean hermit-crab and certain insect-larvæ whose bodies are protected by sheaths, but it seems a little hazardous when applied to the termites. We have here, in the history of the evolution of the soldier, a perplexing unknown quantity—an unexplained hiatus.

The well-known aphorism 'the function makes the organ' accounts for certain variations, and is incontestably applicable to modifications of already-existing parts (the perfecting of the mandibles, for instance), but that does not mean that the function, however desirable, suffices to create a new organ with all its parts.

The first origins of things nearly always elude us.

To take the case of the mole-cricket (*Gryllotalpa*)—does the insect dig in the ground because it has feet suitable for burrowing, or has it acquired such feet because it digs? Since the mole-cricket as we see it is perfectly adapted to its mode of life, the most plausible reply is that the habit of digging in the earth and the corresponding organ developed at the same time (in a parallel fashion).

The same process of reasoning is applicable to insects in general, as soon as their evolution is finished and they are completely adapted to their environment. As for termites, we have the right to conclude that morphological variations go hand in hand with variations in instinct and their improvement.

The evolution of instincts derived from mental dispositions (our third category) will not detain us so long, for the action of natural selection is here easier to understand and less troublesome to explain. It is certainly obvious that a colony of termites which has at its disposal brave soldiers and highly active workers will sooner or later prevail over a

neighbouring colony which is incapable of mustering defenders and workers of the same quality.

A termite-colony whose inhabitants set out to lavish the most attentive care upon the young larvæ will similarly prevail over a neighbouring colony which leaves its unfortunate new-born offspring to disentangle themselves unaided. This is surely an admirable use of natural selection, since, in the cases cited as examples, it is not brute force but the noblest instinct—devotion to the common good—which has finally triumphed in the termite colony.

Just as it is interesting to discover the first gleams of intelligence in the lower animals, and to mount by degrees to the mind of men by way of the elephant, the dog and the anthropoid ape, so is it extremely suggestive to observe the dawn of a moral sense in animals. It is assuredly a moral action when the female orang-outang or gorilla, driven to bay by the hunter, covers her little one with her body in the hope of saving it. And when the soldier-termite, during an attack, allows itself to be killed at the breach, it too achieves an action of incipient morality; and so does the female ant enclosed in a box and left entirely alone to fast for several consecutive months, when she consumes her own substance (fat-body, thoracic muscles) to nourish her young larvæ.

In cases of this kind, it is true, the alleged moral sense may be considered as instinctive, and this diminishes, to a certain extent, its value and beauty. The particular form taken by the psychic life in the insect enables us, however, to explain this phenomenon.

Directly reasoned action on the part of the hexapod tends to be transformed into a habit, we may well assume that spontaneous impulses of an altruistic character, from the fact that they are useful to the community as a whole, will

likewise, thanks to natural selection, become automatic or instinctive. The first soldier-termite which ever allowed itself to be killed in battle set an example which was generalized by imitation among its kind, and which gradually became habitual.

Even in man, the type of man who has been shaped by a firm and effective education, we see some of the noblest virtues, such as a hatred of lies, devotion, generosity and courage, so deeply rooted in his character that they never fail, and become automatic. And no one would dare to affirm that because the moral qualities in question have become automatic in the individual who possesses them, they have therefore lost part of their value!

As for the suggestion that some *mental* and *moral bond* unites the inhabitants of a termitary—it is scarcely possible to compare a colony of insects with a human society. Human groups, even in their primitive state, are commanded by chieftains. The more advanced nations place kings, queens and magistrates at their head. Nothing of this kind happens among the termites. The male and female individuals which are described in the higher termites as *king* and *queen* have no authority and possess no power of any kind. The king and the queen termite, shut in their closed cell, do not even know what is happening outside. It would be impossible for them to give orders from the depth of their prison. The to-and-fro motion of soldiers and workers in the narrow passages leading to the royal compartment has no other purpose than the revictualling of the wedded pair. The functions of the queen and the king termite are limited to the production of eggs and their fertilization.

Nor is it possible, in the soldier and worker castes, to distinguish any individuals which are specially differentiated and which seem superior to the others, comparable to human

officers. But this is not all. Whereas human societies present an extraordinary diversity, manifesting between the bottom and the top of their ladder all stages of intelligence, will and moral value (and also, unfortunately, of coarseness and stupidity), termite societies, on the contrary, present the most complete uniformity. In every caste there is perfect equality, universal levelling, that dream of communists throughout the ages.

But if there are no officers, no superiors to command, how can we explain work in common, continued effort exerted on behalf of the general good? What is the motive force of this understanding which is never, under any circumstances, found to be at fault? In the experiment related above (removal of part of the wall) how are we to explain the agreement which immediately took place between soldiers and workers, urging the one caste to repulse the ants and the other to repair the breach?

We must assume, apparently, that the common activities observed in termites are all the result of unconscious impulses, or, in other words, instinctive automatisms. Every soldier-termite—and every worker must bring into the world, when it is born, certain psychic dispositions resulting from a long process of adaptation. Attached to the brain cells and engraven upon the nervous substance like a kind of memory, these dispositions, which bear the name of instincts, must be transmitted from one generation to the other according to the laws of heredity, in the usual fashion of vital dynamisms. Retaining the definitions proposed by Semon, we call these the engrams of the individual mneme, including also their ecphories or external manifestations.[1]

[1]Richard Semon, *Die Mneme als erhaltendes Prinzip im Wechsel des organischen Geschehens*, Leipzig, 1904 (E.T. *Mneme*, 1922); *Die mnemischen Empfindungen*, 1909. (E.T. *Mnemic Psychology*, 1923).

In intimate relationship with the gradual perfecting of defence-measures, all instincts must have been specialized at the same time in each caste, and transmitted generation by generation to the new-formed individuals.

Against this theory there are admittedly some objections. The asexual termites (workers and soldiers) being generally sterile, it is difficult to understand how new instincts, acquired by individuals of these two castes in the course of the struggle for existence, could be transmitted to the sexual males and females—how, in short, they could become hereditary.

Two hypotheses may be offered:

1 Seeing that ants have their antennal language,[1] we may suppose that the termites can also, under certain circumstances, communicate their impressions to one another.

Highly instructive observations can be made with *Eutermes monoceros*, for example, when the army of this species sends out a squad of soldiers to scout, as a preliminary to the gathering of lichens. The majority of the troop, before setting out on the march and choosing its direction, waits for their return and the 'confidences' they have to bring back.

As the workers and soldiers live in the interior of the apartments in the company of the sexual forms (until the moment of swarming) it is not entirely incredible, judging

[1]With regard to antennal language, I have made a note on the russet brown ant of Ceylon (*Œcophylla smaragdina*) which I think deserves to be cited. When these ants (frequently found inside bungalows) are marching in line along the edge of the ceiling, there are always a few which walk in the opposite direction and tap with their antennæ all those they meet on the way. It is my belief that they 'tell each other' the way to go in order to find food. See also, on the subject of antennal language Forel, *The Social Life of Ants*, Part II, Chap. II, and Part III, Chap. III.

by the above suggestion, that while they are living together, they should exchange a few ideas. As a result of these 'communications' new instincts acquired by the workers and soldiers would become the property of the community as a whole.

2 The second hypothesis, which in my opinion is more plausible, is based chiefly on the differentiation of workers and soldiers in the course of the centuries. Given the fact that the asexual forms are manifestly derived from the sexual, we may quite reasonably assume that the workers and soldiers in the first stage of differentiation were fertile capable of procreation. We still encounter workers and soldiers which are able under certain circumstances to form ovules and sperms.

Dr. Imms, for instance, has dissected soldiers of *Archotermopsis Wroughtoni*, some of which had ovaries full of ovules and others well-developed male genital organs. These soldiers would probably have been capable, in the absence of the ordinary sexual forms, of reproducing their species. Similar observations had previously been recorded by Lespès (1865) with *Leucotermes lucifugus* and by Fritz Müller (1873) and Grassi (1898) with various *Calotermes* species. In *Termes Struchii*, Silvestri observed forty female workers and eight male workers whose genital apparatus was as highly developed as that of the winged individuals. Heath (1902) saw three soldiers of *Termopsis angusticollis* (a Californian species) which had laid eggs.[1]

Given these facts, we have only to conceive of the period

[1]These references are borrowed from the work by Dr. Imms already quoted, 'On the Structure and Biology of *Archotermopsis*.' Space does not permit me to give an account of this author's theory, according to which the differentiation of castes, in termites in general, results from a series of mutations transmitted from one generation to the other in accordance with Mendel's law.

during which the defence-measures were perfected as coinciding with the period during which the workers and soldiers were fertile, in order to render more plausible the hereditary transmission of the improvements in question and of the instincts (neo-form) related to them.

Furthermore, the instincts inherited from the parents would pass, with every new generation, through a kind of latent stage or sleep, corresponding to the larval phase, and only later (after the transformation), when the young termite reaches the stage of the functional soldier or functional worker, would they begin to exhibit outward manifestations.

Thenceforward, since the dispositions attached to the soldier's brain and the dispositions inherent in the worker's brain would be absolutely identical for all members of the same caste, there would result, in each particular case, a succession of actions of never-failing similarity, which could be repeated with practically no variations.

Thus in the case of the sinking of a tunnel (an experiment carried out with *Eutermes* of the cocoa-trees), the sudden irruption of light into the interior would have the result of bringing up to the breach all the soldiers contained in the tunnel, which would run thither from every corner in which they had been surprised by this irruption. Obeying an automatic impulse, these soldiers would arrange themselves of their own accord around the right spot at the surface of the bark, in the defensive attitude peculiar to them.

The irruption of luminous rays, acting to an equal extent upon the workers, would have the effect of exciting them also to fulfil their habitual functions, which consist, in the case in point, in bringing together particles of rubble, moistening them with the contents of the rectum, and mending the wall as soon as possible.

These actions, which give us the impression of being

voluntary and thoughtful, by reason of their co-ordination and their perfect regulation, would thus really be automatic (instinctive).

The multifarious duties which are carried out under our eyes by the soldiers on the one hand and the workers on the other, give us the illusion of a higher direction, whereas in reality this direction does not exist, or, if it does, resides solely in the community as a whole.[1]

Conclusions

From the above considerations I think I am justified in drawing the following conclusions:—

1 The termite colonies, in their present form, are the result of an adaptation to the circumstances in which they have been obliged to develop;

2 This adaptation to circumstances, continued for hundreds and thousands of years, has been largely dominated by the obstinate warfare which the ants force upon the termites;

3 The countless ingenious defence-measures employed by the termites are manifestly one of the consequences of this war;

4 The presence of a highly-differentiated soldier-caste specially organized for defence and attack, can also be explained as a particular form of adaptation to this warfare.

5 The origin of most of these instincts is a reasoned and conscious action;

[1]The alleged 'higher direction' which appears at first to command the colony, is not vested in a few privileged individuals, comparable to chieftains. It would be more exact, if the term is to be kept, to regard the 'higher direction' of the colony as a resultant of the psychic energy of the whole community. It seems certain, however, that the soldier caste possesses a moral authority slightly greater than that with which the other groups (worker and sexual forms) are endowed.

6 If actions of this kind, many times repeated, are useful for the conservation of the species, they tend to merge gradually into habits;

7 Once become habitual, they tend to take place of their own accord, to be transformed into reflexes, in short, to become automatic or instinctive;

8 The instinctive impulses, indelibly engraven upon the brain, have gradually become hereditary;

9 The alleged moral direction which appears at first sight to be commanding the colony does not belong to a few termites which can be compared with chieftains; it is the result of the activity of them all. It appears to be established however, that the soldier-caste possesses a slightly greater authority.

10 The useful instincts, which are subject to the laws of natural selection, just as much as the evolution of the organs, will persist, whereas the useless or harmful instincts will inevitably disappear.

While the life of the insect is dominated by instinctive activities which are usually unconscious, the life of man, apart from a few exceptional cases, is nearly always commanded by his conscience and his reason. The characteristic of the higher type of man is precisely to dominate his instincts and to fight them if they are bad.

Instinctive activity, as soon as it is fixed for any insect, varies very little; it is transmitted from one generation to another in practically the same form; hence the uniformity found in ants and termites with regard to the behaviour peculiar to individuals of each caste. But, in strong contrast with insect communities, human societies are distinguished from the bottom of the social ladder to the top, by the extraordinary diversity of the individuals composing it

and by a perfectibility which, despite the disappointments of the moment, justifies us in hoping for better times.

Is it not man's perfectibility which distinguishes him from the animal and is the *raison d'être* of humanity? And is it not this undeniable perfectibility which remains proof against the worst trials, and enables human beings to create an ideal and to look for ever upwards?

FINIS.

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